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A NEW SEQUOIOXYLON FROM FLORISSANT, COLORADO[1]

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The Miocene lake bed at Florissant, Colorado, has long been recognized for its wealth of fossil plants, insects, and vertebrates. The excellence of the leaf impressions found in these sedimentary deposits is second to few localities in the world and certainly the silicified trunks and stumps, at least as regards size, are unsurpassed. The Florissant flora has been generally accepted by competent paleobotanists as being of Miocene age (Berry, '29, p. 234). More recently, Gazin ('35), in describing a marsupial *(Peratherium* sp.) from this formation, suggests a lower Tertiary age. The weight of evidence at present, however, is in support of the Miocene.

Of the score or more of stumps that have been excavated at the Henderson Petrified Forest (located $2\frac{1}{2}$ miles south of Florissant) one in particular is outstanding because of its magnitude. The stump was mentioned by Gordon ('34) in a recent address before the British Association as follows: "The largest fossil tree I know, and I think it is the largest yet discovered, is a stump said to be of the *Sequoia* type. . . . It is $17\frac{1}{2}$ feet in diameter and 10 feet high, quite comparable in girth, therefore, with the Big Trees of today." Henderson ('06) writes of the abundance of fossil stumps at Florissant and figures one, said

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to be a *Sequoia,* which unquestionably is the same one mentioned by Gordon and described in this paper (pl. 20, fig. 1). According to Henderson, unsuccessful attempts were made to cut sections of the trunk for exhibition purposes.

Apparently no anatomical studies of this stump have ever been published despite its unusual interest. The wood is infiltrated with silica and only slightly replaced, the preservation being very good with the exception of the pitting in the radial walls of the ray cells. A few ground sections were prepared, but due to the fragility of the wood satisfactory transverse sections could not be obtained by the usual method. Consequently, small fragments were desilicified in a solution of ⅓ hydrofluoric acid and ⅔ alcohol for 3–4 days, then embedded in celloidin, and cut on a sliding microtome. Very satisfactory transverse sections were obtained using this method, but desilicification rendered the radial sections of less value than the ground ones.

SEQUOIOXYLON PEARSALLII, N. SP.

Annual rings.—Well-defined, comprised mostly of large, thin-walled cells, the greater portion of which have been crushed (pl. 20, fig. 3); relatively little summer wood, transition varying from abrupt (pl. 21, fig. 7) to gradual (fig. 6).

Resin canals.—Neither normal nor traumatic resin canals observed.

Wood parenchyma.—Abundant, more so in late spring and summer wood, diffuse, resinous; cells markedly smaller in diameter than surrounding tracheids.

Wood rays.—Few to 30 or more cells high, mostly uniseriate, occasionally biseriate; apparently one to two pits per cross field although the preservation of this feature is very poor, horizontal walls sparingly pitted but no pitting observed in cross (tangential) walls; marginal ray cells larger and more nearly resembling true ray tracheids than the ray parenchyma, also entirely lacking the resinous (?) contents of the latter (text-fig. 1).

Tracheids.—Pitting uniseriate (mostly scattered) and biseriate (usually opposite); crassulae not observed; tangential

pitting abundant in late summer wood (pl. 20, fig. 5). Strand tracheids occasionally found in summer wood composed of short tracheary elements interspersed with parenchyma cells, both horizontal and *vertical* septations occur, the vertical septations always extending in a radial direction (pl. 20, fig. 4, pl. 21, fig. 9).

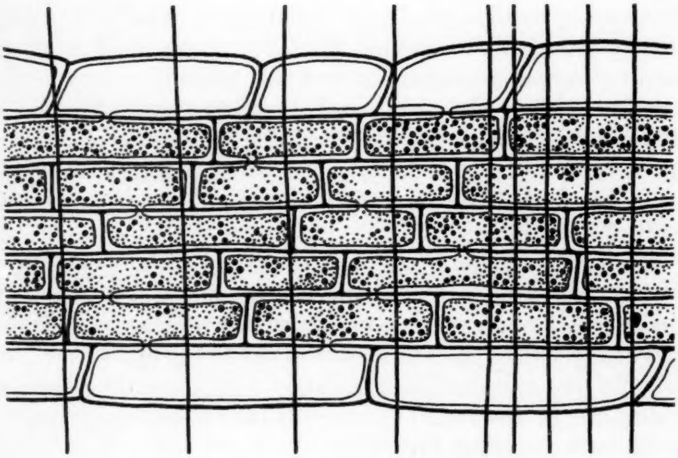


Fig. 1. *Sequoioxylon Pearsallii.* Radial longitudinal view of ray, showing pitting of horizontal walls and differentiated marginal cells.

The species is named for Mr. Cortland Pearsall, of the Massachusetts Institute of Technology, for his valuable assistance in the field and laboratory.

With the exception of the ray structure the general anatomy of the wood indicates a close relationship to *Sequoia,* and although traumatic resin canals have not been observed we feel justified in placing the wood in the genus *Sequoioxylon.* The two most interesting and distinctive features of this wood are the ray structure and the presence of strand tracheids.

The strand tracheids, with their horizontal and *radio-longitudinal* septations composed of short tracheary elements interspersed with parenchyma cells, are, to the writer's knowledge,

a previously undescribed feature in fossil woods. Dr. I. W. Bailey ('34) has described uniseriate strand tracheids in the living redwood *(Sequoia sempervirens)* and has kindly advised the writer that the biseriate type (pl. 20, fig. 4; pl. 21, fig. 9) is of common occurrence in injured crowns of that tree, but apparently figures of the feature have never been published. A band of the strand tracheids is shown in tangential view in the late summer wood in pl. 21, fig. 8 and portions of the same are shown more highly magnified in pl. 20, fig. 4 and pl. 21, fig. 9. The longitudinal septations extend only radially as may be seen by their complete absence in radial section (pl. 20, fig. 2). As this feature is not of constant occurrence at the end of every ring it is doubtful whether it is of any phylogenetic significance; it is more likely that the longitudinal septations are the result of traumatism.

The differentiation of the marginal ray cells is a constant feature and not merely of sporadic occurrence as in the living *Sequoia*. Although not true ray tracheids they are usually distinctly larger than the remainder of the ray cells, more nearly resemble true ray tracheids in shape, and are entirely lacking the ergastic or resinous (?) contents characteristic of most of the ray cells (text-fig. 1).

The wood under consideration seems to resemble *Sequoia Penhallowii* Jeffrey more closely than any other described species of Sequoian affinities. Our specimen differs, however, from *S. Penhallowii* not only in its lack of horizontal and vertical resin canals, but also in a greater abundance of wood parenchyma and lack of pitting in the tangential walls of the ray cells. Undoubtedly we are dealing with a transitional form between the old Abietinean stock and the present-day Sequoias, although, to be sure, the wood described here is much closer to the living *Sequoia* than their Abietinean ancestors.

Like most of our fossil forests the one at Florissant seems to have been rather badly neglected as regards detailed anatomical studies of the silicified stumps and trunks. It would seem that a study of the annual rings of some of the larger specimens might throw some light on the climatic conditions existing there during the Miocene.

Literature

Bailey, I. W. ('34). The cambium and its derivative tissues. IX. Structural variability in the redwood. Jour. Arn. Arb. **15**: 233–254.

Berry, E. W. ('29). A revision of the flora of the Latah formation. U. S. Geol. Survey, Prof. Paper 154: 225–266.

Cockerell, T. D. A. ('06). The fossil fauna and flora of the Florissant (Colorado) shales. Univ. Colo. Stud. **3**: 157–176.

———, ('08). The fossil flora of Florissant, Colorado. Am. Mus. Nat. Hist. Bull. **24**: 71–110.

———, ('10). The Miocene trees of the Rocky Mountains. Am. Nat. **44**: 31–47.

Gazin, C. L. ('35). A marsupial from the Florissant beds (Tertiary) of Colorado. Jour. Paleontol. **9**: 57–62.

Gordon, W. T. ('34). Plant life and the philosophy of geology. Brit. Assn. Adv. Sci. Rept. **104**: 49–82.

Henderson, J. ('06). The Tertiary lake bed of Florissant, Colorado. Univ. Colo. Stud. **3**: 145–156.

Jeffrey, E. C. ('04). A fossil Sequoia from the Sierra Nevada. Bot. Gaz. **38**: 321–332.

Kirchner, W. C. G. ('98). Contribution to the fossil flora of Florissant, Colorado. St. Louis Acad. Sci. Trans. **8**: 161–188.

Torrey, R. E. ('21). Telephragmoxylon and the origin of wood parenchyma. Ann. Bot. **35**: 73–77.

———, ('23). Comparative anatomy and phylogeny of the Coniferales. Part 3. Mesozoic and Tertiary coniferous woods. Bost. Soc. Nat. Hist. Mem. **6**: 41–106.

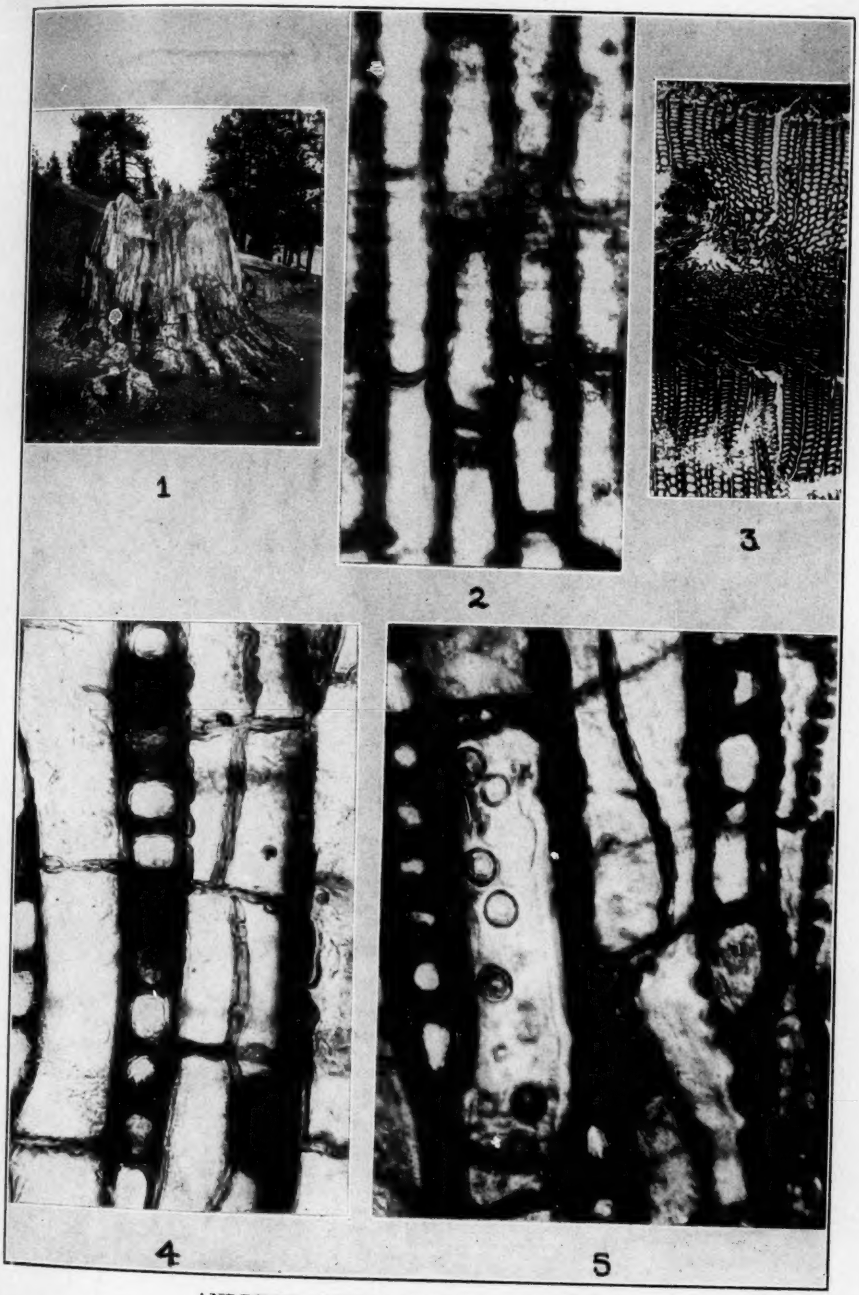
Warder, R. B. ('83). The silicified stumps of Colorado. Am. Assn. Adv. Sci. Proc. **31**: 398–399.

Explanation of Plate

PLATE 20

***Sequoioxylon Pearsallii*, n. sp.**

Fig. 1. Photograph of the stump, Henderson Petrified Forest, Florissant, Colo.
Fig. 2. Radial view of the strand tracheids.
Fig. 3. Transverse section through two annual rings.
Fig. 4. Tangential view of strand tracheids.
Fig. 5. Tangential view showing tangential pitting in late summer tracheids.



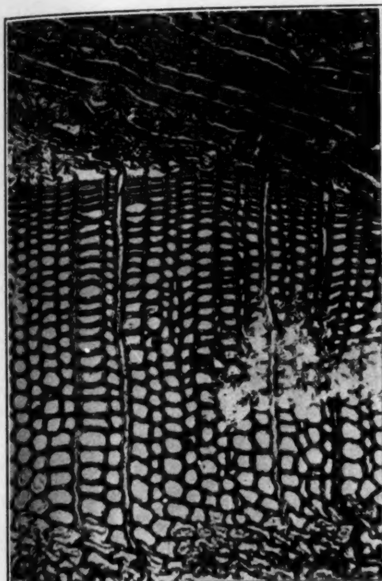
ANDREWS—SEQUOIOXYLON PEARSALLII

Explanation of Plate

PLATE 21

Sequoioxylon Pearsallii, n. sp.

Fig. 6. Transverse section showing gradual transition.
Fig. 7. Transverse section showing abrupt transition.
Fig. 8. Strand tracheids in late summer wood.
Fig. 9. Portion of same more highly magnified.



6.

7.

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9.

ANDREWS—SEQUOIOXYLON PEARSALLII

FIELD AND HERBARIUM STUDIES, IV[1]

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Picea pungens (Parry) Engelm., Gard. Chron. N. S. **11**: 334. 1879.

During the past three preceding summers occasion was had to study the distribution of the Blue Spruce in Wyoming, of which there is probably a great deal more than is generally realized.

It extends, so far as was observed, along the Snake River, from Jackson Lake, in Teton County, at least to the Gorge of the river in Lincoln County, as well as up all of the tributary creeks and rivers. Along the Snake River, some fifty miles, it is the predominant conifer and is exceedingly abundant, but along the tributaries which usually gain elevation rather rapidly it is of less importance. In Sublette County it was found around Fremont Lake, Half Moon Lake, and other of the lakes in that vicinity. It is also to be found along the Green River but there it is not common. It does not ascend the river as far as the Green River Lakes; whether or not it goes farther down the river than a point due west of Pinedale is not known. The tree is also to be found, in this county, along the Hoback River which is a tributary of the Snake River. In Fremont County it was first observed near Dubois on the Wind River and extends up that river from there for several miles, and is also on some of the tributary streams. How generally it is distributed along the other creeks or how far it may extend down the east side of the Wind River Mountains remains to be investigated.

Acquaintance with the tree in Colorado does not quite give one an adequate idea of the species as it occurs in northwestern Wyoming. At first sight it may not be realized that it is the Blue Spruce. It is almost entirely lacking in any "blue cast." Again it is to be found only along the streams or at most no great distance from the water. The size attained is much

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greater than any the author has seen in Colorado. Trees four to five feet in diameter at shoulder height are not uncommon; one measured just under six feet in diameter. The height is in proportion.

The altitudinal limits seem to be rather definite. It is rarely found above 7500 feet altitude and so far as observed not below about 5700 feet. The best development is between 6000-7000 feet in Teton County. In this region the Blue Spruce is often associated with the Engelmann Spruce *(Picea Engelmannii* Parry). One tree, in such an association, observed above Dubois had cones which seemed to be intermediate both in size and in shape of the cone scales between the two species, but inclining slightly more toward those of the Blue Spruce. Cones observed from a tree on the grounds of the Lee Ranger Station, near Wilson, showed a large range of variation, particularly in shape of the cone scales but cones were not so small as on the tree near Dubois.

Salix Tweedyi (Bebb) Ball, Bot. Gaz. **40**: 377. 1905.

This willow was found in abundance along Cascade Creek, one of the cold glacial streams in Grand Teton National Park. During the past summer it was found again in the Big Horn Mountains of Wyoming where the original collection was made. From Dr. Carleton R. Ball, who has kindly determined the material, comes the information that sets of this species have not been distributed among herbaria. My numbers 1133, 1668, and 1686 show it in various stages of development.

Specimens were collected in a spruce bog near Bald Mountain, elev. 9500 ft., Big Horn Co., Aug. 29, 1935, *Williams 2511.*

Salix cascadensis Ckll., Muhlenbergia **3**: 9. 1907.

This plant is quite common in Grand Teton National Park, between 9500 and 11,000 feet altitude, where it covers acres of ground. My numbers 915 and 1352, determined by Dr. Ball, illustrate it.

Salix arctica Pallas, Fl. Ross. I. **2**: 86. 1784–1788.

This species is not mentioned in Rydberg's 'Flora of the Rocky Mountains and Adjacent Plains' or in the Coulter and

Nelson 'Manual of Rocky Mountain Botany.' It is found occasionally in Grand Teton National Park. My number 1708, determined by Dr. Ball, represents it.

Populus taccamahacca Miller, Gard. Dict. ed. 8. Populus No. 6. 1768.

Both the broad- and narrow-leaved forms are found in Teton County, Wyoming. The narrow-leaved form occurs along the streams in the valley. The broad-leaved form, which Dr. Alfred Rehder has kindly determined and which he informs me was not previously in the collection of the Arnold Arboretum from Wyoming, is to be found in the canyons of the Teton range.

Xerophyllum tenax (Pursh) Nutt., Gen. **1**: 235. 1818.

This genus seems not to have been reported from the state of Wyoming. Two specimens are at hand, both sent to the author for determination and both from Teton County (slope north of Jackson Lake, July 11, 1932, *W. B. Sheppard;* four miles west of Cascade Creek on the road to Ashton, Idaho, along Reclamation Road, June 25, 1934, *Mrs. J. W. Orlob 1633b).*

Professor Nelson, in Coulter and Nelson's 'Manual of Rocky Mountain Botany,' p. 118. 1909, states the range as: "Montana, possibly Wyoming, and west to Oregon." In a letter he informs me that there are no specimens in the Rocky Mountain Herbarium collected in Wyoming.

Paeonia Brownii Dougl. in Hook., Fl. Bor. Am. **1**: 27. 1829.

The published floras covering the Rocky Mountain region do not give this genus as occurring in Wyoming, yet several specimens from the northwestern part of the state have been in existence since 1860. More recently several collections have been made from the same area, of which the following may be cited: Jackson's Hole, on Snake River, June 18, 1860, *F. V. Hayden;* on Henry's Fork, June 19, 1860, *F. V. Hayden;* Lake Fork, June 22, 1860, *F. V. Hayden;* gravel flats, Jackson's Hole, Aug. 3, 1920, *Payson & Payson 2169;* near Jenny Lake, Grand Teton National Park, 1931, *Mrs. A. C. Lyon;* gravel flats near Jenny Lake, Sept. 2, 1933, *Williams 1434.*

The Hayden specimens were sent to Dr. Engelmann for determination but were not included in the published list of the plants of that expedition. They bear no annotations by Dr. Engelmann.

Aquilegia Jonesii Parry, Am. Nat. **8**: 211. 1874.

This rare columbine was found again in the Big Horn Mountains. It seems to inhabit only the calcareous rock slides. My number 2358, July 5, 1935, represents it.

Roots and seeds were sent to the Cheyenne Horticultural Field Station at Cheyenne. It will be of interest to see if it survives in cultivation.

Ranunculus jovis A. Nels., Bull. Torr. Bot. Club **27**: 261. 1900.

While the rocky flats of Grand Teton National Park were in most places still covered with two feet of snow and the temperature was below the freezing point each night this little plant was thriving. Indeed it had nearly matured its seed before the snow was gone from the flats. It is of interest to find this at an elevation as low as 7000 feet, since it is usually to be found in the alpine regions. (*Williams & Pierson 1074,* April 24, 1933, distributed as *R. glaberrimus* Hook.?).

Thermopsis rhombifolia (Nutt.) Rich., var. **annulocarpa** (A. Nels.), comb. nov.

T. annulocarpa A. Nels., Bull. Torr. Bot. Club **26**: 239. 1899.

Professor Nelson in Coulter and Nelson's, 'Manual of Rocky Mountain Botany,' p. 271. 1909, referred this to *T. rhombifolia* as a synonym. However, it seems to merit varietal rank even though the characters by which it is distinguished are superficial. There seems to be another closely related variety of the species occurring on the western border of the range. Whether it represents an undescribed variety or is *T. arenosa* A. Nels. will have to await a study of the type of that species.

Dalea Grayi (Vail), comb. nov.

D. laevigata Gray, Pl. Wright. **2**: 38. 1853, non Sesse & Moc. 1832.

Parosela Grayi Vail, Bull. Torr. Bot. Club **24**: 14. 1897.

Thornbera Grayi Rydb., N. Am. Fl. **24**: 119. 1920.

Dalea Thompsonae (Vail), comb. nov.

Parosela Thompsonae Vail, Bull. Torr. Bot. Club **24**: 18. 1897.

Among a fine collection of plants received from Mr. Bertrand Harrison for determination is a specimen which seems, *ex char.*, to be referable to this species. If the determination is correct it represents a considerable extension of range. The specimen bears the following data: dry sandy wash, excessively alkaline soil, Henry Mountains, Vanadium Mine, Garfield Co., Utah, May 20, 1934, *Harrison 7520.*

Hoffmanseggia tenella B. C. Tharp & L. O. Williams, n. sp.[2]

Slender perennial herb, 8–15 cm. tall; stem proper short, unbranched or nearly so, terminated by a few-flowered simple raceme; leaves bipinnate with 3–7 pinnae, as long as or exceeding the inflorescence, sparingly soft-pubescent, the petioles 5–13 cm. long; the pinnae with 5–6 pairs of pinnules, the pinnules sessile on the rachis or nearly so, 2–4 mm. long, 1–2 mm. broad, oblique, glabrous on the upper surface, sparingly pubescent on the lower surface and margins; stipules small, scarious, 1–2 mm. long, adnate to the petiole; inflorescence not exceeding the leaves, usually 3–5-flowered, each pedicel subtended by a short scarious bract; calyx about 4 mm. long, the lobes linear-oblong, obtuse, slightly naviculate, finely but densely pubescent; petals obovate, attenuated into a very short claw, 3–4 mm. long, 1.5–2 mm. wide; filaments free, with a few short hairs; mature legume 12–15 mm. long, 4–6 mm. wide, straight, finely and rather densely pubescent but not glandular; seeds 2–4.

Texas: Robstown to Alice, Nueces Co., Nov. 22, 1931, *Mrs. F. E. Clements 128b* (Herb. Univ. Texas, type; fragment and photograph of type in Herb. Mo. Bot. Gard.).

This species seems to have its nearest ally in *H. drepanocarpa* Gray, from which it differs in several aspects. The

[2] **Hoffmanseggia tenella** B. C. Tharp & L. O. Williams, n. sp., herba perennis gracilis, 8–15 cm. alta, simplice aut sparse ramosa; inflorescentiis paucifloris terminalibus; foliis bipinnatis, 3–7 pinnis, pubescentibus vel fere glabris, 5–6 paribus foliolarum; stipulis parvis, 1–2 mm. longis; calyce fere 4 mm. longo, pubescente, lobis lineari-oblongis; petalis obovatis, 3–4 mm. longis, 1.5–2 mm. latis; legumine 12–15 mm. longo, 4–6 mm. lato, recto, pubescente, sine glandulis.

leaves of the latter have 7–11 pinnae, those of ours have 3–7. In *H. drepanocarpa* the inflorescence usually exceeds the leaves and has several flowers, while in our plant it rarely if ever exceeds the leaves and the flowers are fewer. The legume of that species is 25–40 mm. long and is strongly falcate, while that of ours is about half or less that length and straight. Our plant is noticeably more slender than *H. drepanocarpa* and has fewer stems to the root.

Dryas Drummondii Richards., var. **tomentosa** (Farr), comb. nov.

D. tomentosa Farr, Ottawa Nat. **20**: 110. 1906.

That this can be maintained as a distinct species on its rather meagre characters is doubtful. Juzepczuk, in Bull. Jard. Bot. URSS. **28**: 311. 1929, places it in a new section, Nothodryas, of *Dryas,* along with *D. Drummondii* Richards. and *D. grandis* Juz. With the former, at least, it is closely related, but the latter has not been seen.

It is of interest to note that Juzepczuk, *l.c.* p. 325, describes a new species, *D. Hookerianum* from Rocky Mountain material. The writer is unable to find specific or even varietal differences between available material, which he cites, and European material of *D. octopetala* L.

Zauschneria Garrettii A. Nels., Proc. Biol. Soc. Wash. **20**: 36. 1907.

Z. latifolia var. *Garrettii* Hilend, Am. Jour. Bot. **16**: 66. 1929.

Finding this species above Bradley Lake in Grand Teton National Park came as a distinct surprise to the author. However, on looking up the distribution of the species several collections were found which were out of the range, "in mountains of Utah and southern Wyoming," given by Miss Hilend in her revision of the genus. The only specimen cited for Wyoming in that revision is from west-central, not southern, Wyoming. The following specimens may be cited:

Wyoming: hills east of Afton, Aug. 8, 1923, *Payson & Armstrong 3771;* ledges above Bradley Lake, Grand Teton National Park, Aug. 14, 1933, *Williams 1403;* mountains west of Cody,

Park Co., July, 1905, *Worthley;* mountain top, Holm Lodge, about 40 miles west of Cody, Aug. 26, 1922, *von Schrenk.*

Rhododendron Warrenii Macbr., Contr. Gray Herb. N. S. No. 56, p. 55. 1918.

Azaleastrum Warrenii A. Nels., Bot. Gaz. **56**: 67. 1913.

A consideration of the type and two subsequent collections of this species from Colorado, contained in the Rocky Mountain Herbarium and kindly loaned the author for study, raises a question concerning the taxonomic status of the species.

The collection on which the species is based is rather meagre; however, the description given for it is accurate. It compares very favorably with the abundant material at hand of *R. albiflorum* Hook., Fl. Bor. Am. **2**: 43. 1834 *(Azaleastrum albiflorum* Rydb., Mem. N. Y. Bot. Gard. **1**: 297. 1900), from the northwest in a similar stage of development.

An excellent collection, mountains due west of Walden, July 20, 1930, *Leonard Johnson,* from the same region, perhaps type locality, leaves little doubt that the plants are the same as those from the Northwest. The several hundred miles between the Colorado station and the nearest known station in Montana raises an interesting question in distribution.

Dr. Rydberg gave the distribution and range of *Azaleastrum Warrenii,* in the 'Fl. Ry. Mts. and Adj. Plains,' p. 640. 1917, as "Mountain slopes: Colorado." However, so far as it is known, it seems to occur only at the station at which it was first collected and near by, not nearly as widely distributed as Dr. Rydberg's note would indicate. The three specimens in the Rocky Mountain Herbarium are all from Jackson County.

Nemophila petrophila n. sp.[3]

Low annual, 4–13 cm. tall; cotyledonary leaves persistent, opposite, obovate to oblanceolate, entire, 1–2 cm. long, 4–6 mm.

[3] **Nemophila petrophila** n. sp., annua humilis 4–13 cm. alta; foliis cotyledonium oppositis, obovatis vel oblanceolatis, 1–2 cm. longis, 4–6 cm. latis, integris, infra glabris; foliis caulium ovatis, 1–2 cm. longis, pinnatis, lobis ovatis, integris, utrinque strigosis; floribus axillaribus; calyce fere ad basin diviso, lobis lineari-lanceolatis, 3–5 mm. longis, ciliatis; appendicibus in sinu 0.5–1.5 mm. longis; corolla fere 2 mm. longa.

broad, glabrous below, the petioles joined and sheathing the stem; cauline leaves opposite or rarely alternate, ovate in outline, 1–2 cm. long, 3–5-pinnate, the lobes ovate, entire, sparingly strigose on both surfaces; flowers usually one from the axils of the upper leaves; calyx 3 mm. long in flower, about 5 mm. long in fruit, divided almost to the base, the lobes linear-lanceolate, long-ciliate, otherwise glabrous or nearly so; reflexed appendages in the sinuses of the calyx lobes 0.5–1.5 mm. long, ciliate; corolla campanulate or apparently tubular, about 2 mm. long, shorter than the calyx-lobes, destitute of any appendages within, lobes ovate, about half of the length of the corolla; stamens attached near the base of the corolla by very slender filaments, barely reaching the orifice of the corolla; style 0.5–0.75 mm. long, enlarged and lobed at the apex but not divided; ovules two on each fleshy placenta, only one maturing; mature capsule round, 3–4 mm. in diameter, sparingly pubescent; seed round, 2.5–3 mm. in diameter, roughened or scarred at the apex, otherwise smooth, dull brick-red, solitary, filling the capsule.

WYOMING: rocky flats under *Pinus contorta*, Double Diamond Ranch, Grand Teton National Park, June 3, 1935, *Williams 2172*, TYPE; rocky open flats near Sensenbach's ranch, Grand Teton National Park, June 8, 1933, *Williams 1094*; Jackson's Hole, on Snake River, June 12, 1860, *Hayden;* marly soil, Jackson's Hole, June 14, 1860, *Hayden;* gravelly soil, Jackson's Hole, June 12, 1860, *Hayden;* rich marly hills, Jackson's Hole, in the valley of the Snake River, *Hayden*. All specimens cited in Herb. Mo. Bot. Gard.

This species seems to have its nearest allies in *N. parviflora* Dougl. and the closely related entities of that species as treated by Brand in 'Pflanzenreich,' Heft 59, IV. 251, pp. 54–55. 1913. It is quite common on the sagebrush flats in the region cited. The other species of the genus, *N. breviflora* Gray, which occurs in the mountains and in the same region as *N. petrophila* but along the moist swales and creek banks in the shade is quite distinct. Specimens of the proposed species were first collected by Hayden 76 years ago, but it seems not to have been found again until recently.

Penstemon aridus Rydb., Mem. N. Y. Bot. Gard. **1**: 348. 1900.

Apparently the first known collections of this species for Wyoming were made by the author during the summer of 1935. Dr. F. W. Pennell, in his treatment of the genus (Contr. U. S. Nat. Herb. **20**: 313–381. 1920), which covers Wyoming, did not include it. Rydberg in 'Fl. Ry. Mts. and Adj. Plains' gives the range as "Montana." The plant is quite abundant in the Big Horn Mountains. The two following collections are to be referred here: dry hillsides, lower Ten Sleep Canyon, Washakie Co., July 3, 1935, *Williams 2321;* dry western slopes of the Big Horn Mountains, ten miles east of Kane, Big Horn Co., July 5, 1935, *Williams 2348.*

Penstemon Caryi Pennell, Contr. U. S. Nat. Herb. **20**: 354. 1920.

Excellent specimens of this rare species were secured in the Big Horn Mountains, where the type was collected. Dry western slopes of the Big Horn Mountains, ten miles east of Kane, Big Horn Co., July 5, 1935, *Williams 2349.*

Pedicularis cystopteridifolia Rydb., Mem. N. Y. Bot. Gard. **1**: 365. 1900.

This rare and seldom collected species was found to be quite abundant in the Big Horn Mountains of Wyoming at elevations of 8000 feet and above, along the road between Dayton and Kane. In the field it shows a striking contrast to its near allies, *P. scopulorum* Gray, and *P. Hallii* Rydb. Number 2355 of my collections represents it.

Downingia brachyantha (Rydb.) Nels. & Macbr., Bot. Gaz. **55**: 382. 1913.

Moist clay ditch banks, Evanston, Uinta Co., Wyoming, June 21, 1934, *Harrison & Larsen 7933.* This seems to represent the first reported collection of this genus for Wyoming.

Microseris nigrescens Henderson, Bull. Torr. Bot. Club **27**: 348. 1900.

Dr. S. F. Blake, who has kindly determined my Compositae (except Senecio) collected during the past summer, informs me that this has been rarely collected. It is not uncommon in

moist meadows in the Big Horn Mountains and is represented by my number 2339, collected in moist meadows near Powder River Pass, Johnson Co., elev. 9000 ft., July 4, 1935.

Senecio Harbourii Rydb., Bull. Torr. Bot. Club **33**: 158. 1906.

Dry western slopes of the Big Horn Mountains, 10–15 miles east of Kane, Big Horn County, elev. 8000 ft., July 5, 1935, *Williams 2351*.

Dr. J. M. Greenman, who has kindly determined my Senecios, tells me that this seems to be the first recognized collection of this species in Wyoming. It extends the range of the species some 300 miles northward.

Senecio spartioides Torr. & Gray, var. **Fremontii** (Torr. & Gray) Greenman, comb. nov.

Senecio filifolius Nutt. β *Fremontii* Torr. & Gray, Fl. N. Am. **2**: 444. 1843.

Sandy hills near Hat Creek, Niobrara Co., Wyoming, *Williams s.n.*

This interesting variety of *S. spartioides,* although previously collected in Wyoming, seems not to have been reported hitherto for the state.

Specimens of all collections mentioned in this paper are to be found in the Herbarium of the Missouri Botanical Garden unless otherwise noted. Sets of my own collections have been or will be distributed to several American and European herbaria.

THE SPECIES PROBLEM IN IRIS

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I. Introduction

As a biological phenomenon the species problem is worthy of serious study as an end in itself, and not as a mere corollary to work in some other field. It is, to be sure, a problem so fundamentally important that it touches many such fields. Workers in any one of these are humanly prone to regard the evidence from that field as all important and its techniques as all sufficient (particularly if they are themselves unacquainted with other aspects of the problem). When, however, one takes up the problem, *as a problem,* and studies it from the diverse viewpoints of genetics, taxonomy, cytology, and biometry, he realizes that he not only needs most of the existing techniques but that he must devise new ones as well.

Iris versicolor and *Iris virginica* were chosen for such a study since they customarily grow in colonies containing many individual plants; a peculiarity which facilitates the location and study of large numbers of individuals. A preliminary analysis of the problem ('28) and a discussion of certain points connected with the distribution of these species ('33) have already appeared. The following series of papers constitutes a final comprehensive report. The central core of information is an analysis of a precise morphological census of the two species (section IV). For the interpretation of this morphological data it has been necessary to undertake correlated investigations in cytology, taxonomy, glacial geology, and genetics. A technical taxonomic treatment of these irises, together with the related *Iris setosa,* is assembled in section II, although material indirectly of taxonomic interest will be found in sections III and V. The phylogenetic relationship of *Iris versicolor* to *Iris virginica* has proved to be somewhat ex-

ceptional though it is by no means unique among the higher plants. The case has been presented in detail in section III as an example of reticulate relationship. Finally in section V the general problem of evolution in the genus *Iris* is discussed in the light of all the above information.

The major portion of these investigations has been carried out at the Missouri Botanical Garden and at the Arnold Arboretum of Harvard University. A fellowship from the National Research Council enabled me to acquire cytological and statistical techniques for continuing the work. During this time I was a guest of the John Innes Horticultural Institution and of the Rothamsted Experiment Station. A two-months' leave of absence from Harvard University in 1932 made it possible to study with Dr. Sewall Wright at the University of Chicago. Dr. Wright, Prof. J. B. S. Haldane, and Dr. R. A. Fisher have greatly furthered the final analysis of the data, though they are in no way responsible for the imperfections of the work or of its presentation. To the above individuals and institutions grateful acknowledgment is made for these exceptional opportunities. I am indebted to the University of Chicago Press and to Dr. J. Paul Goode for the base maps used in the second paper of this series and to Mr. Fred A. Barkley for figs. 2 and 13.

Bibliography

Anderson, Edgar ('28). The problem of species in the northern blue flags, *Iris versicolor* L. and *Iris virginica* L. Ann. Mo. Bot. Gard. **15**: 241–332.

————, ('33). The distribution of *Iris versicolor* in relation to the post-glacial Great Lakes. Rhodora **35**: 154–160.

II. The Taxonomy of the Northern Blue Flags

As a matter of convenience the essential facts in regard to the nomenclature, classification, and distribution of *Iris versicolor* and its relatives are summarized below. Such a segregation of the taxonomic aspects of the problem is essentially artificial and is dictated largely by practical considerations. Material of considerable taxonomic significance will be found throughout the other papers of this series. Attention is called in particular to pages 476 to 480, 495 to 496, and 501 to 506.

For the loan of material for study the author is indebted to the Curators of the following herbaria: Gray Herbarium, University of Wisconsin, Missouri Botanical Garden, United States National Herbarium, University of Pennsylvania, and the Canadian National Herbarium.

KEY TO THE NORTHERN AND SUB-ARCTIC BLUE FLAGS

A. Seeds with a conspicuous raphe; petals setose, less than 2 cm. long.
- B. Stem short, usually unbranched; natives of eastern North America.... ....*I. setosa* var. *canadensis*
- BB. Stem various, often branched; natives of Asia and western North America.
  - C. Bracts often exceeded by the pedicels; stem usually branched; natives of central Alaska..............................*I. setosa* var. *interior*
  - CC. Bracts exceeding the pedicels; natives of Asia and the northwestern coast of North America..................................*I. setosa*

AA. Seeds with an inconspicuous raphe or none; petals laminate, more than 2.5 cm. long.
- B. Seeds D-shaped, sometimes with an inconspicuous raphe; surface of seed vernicose, regularly pitted; valves of the mature seed capsule reflexed but slightly, if at all; sepals minutely papillate at base of blade; outermost bracts of the inflorescence darker and somewhat vernicose along their margins.............................*I. versicolor*
- BB. Seeds round or D-shaped, without a raphe; surface of seed not vernicose, pitting irregular; valves of the mature seed capsule strongly reflexed; sepals macroscopically pubescent at base of blade; outermost bracts of the inflorescence with undifferentiated margins.
  - C. Seed capsules globose or subglobose; natives of the Atlantic seaboard..*I. virginica*
  - CC. Seed capsules at least twice as long as broad; natives of the Mississippi Valley..............................*I. virginica* var. *Shrevei*

Issued August 10, 1936.

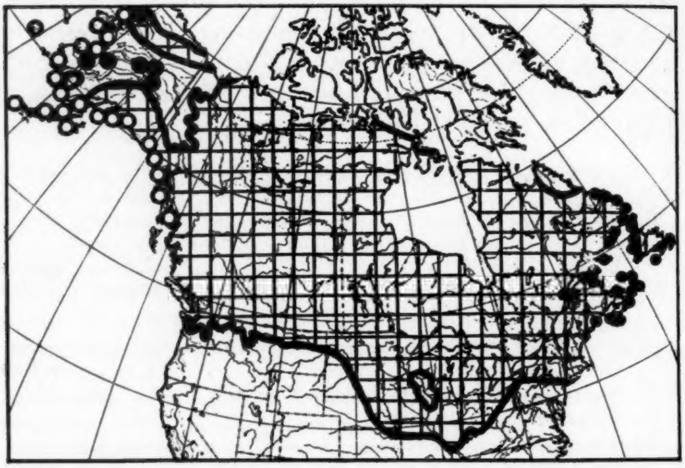
IRIS SETOSA

Iris setosa Pall. ex Link in Spreng., Schrad. u. Link, Jahrb. d. Gewächskunde 1^3: 71. 1820.

Iris arctica Eastwood in Bot. Gaz. **33**: 132, *fig. 2.* 1902.

From coastal Alaska to the Lower Lena River and southwards to Japan.

Perennial from a superficial or underground rhizome; rhizome stout, thickly clothed with the fibrous remains of old leaves; leaves narrowly ensiform to linear, 9–65 cm. long, 0.5–



Map. 1. Range of *Iris setosa* (open circles), *I. setosa* var. *canadensis* (small solid circles), and *I. setosa* var. *interior* (large solid circles). Cross hatching shows extent of maximum Pleistocene glaciation.

1.7 cm. wide; stem slender to stout, 1–5 dm. high, unbranched or with one or two secondary branches, the latter *not exceeding the main axis;* upper cauline leaves *seldom equalling the inflorescence;* inflorescence a compact, 1–3-, mostly 2-, flowered fascicle; bracts of the inflorescence foliaceous to scarious, 3.5–8 cm. long; pedicels slender, exceeding the bracts or exceeded by them; sepals 4–6 cm. long; haft broad, the margin undulate; blade 3–5 cm. wide, *glabrous even at the base,* dark blue-violet (occasionally wine-colored) with *dark veins on a lighter ground-color;* petals small, *setose;* ovary short, 1–2 cm. long in

the flower, *conspicuously three-angled, inflated at anthesis;* capsule short-cylindric to ovate, *symmetrical, highly vernicose* within, often persisting on the plant for one or two years; seeds small, D-shaped, *with a conspicuous raphe, highly vernicose* over minute *regular pitting; chromosomes 38* (2n).

IRIS SETOSA VAR. CANADENSIS

Iris setosa Pall. var. **canadensis** Foster in Rhodora **5**: 158. 1903.

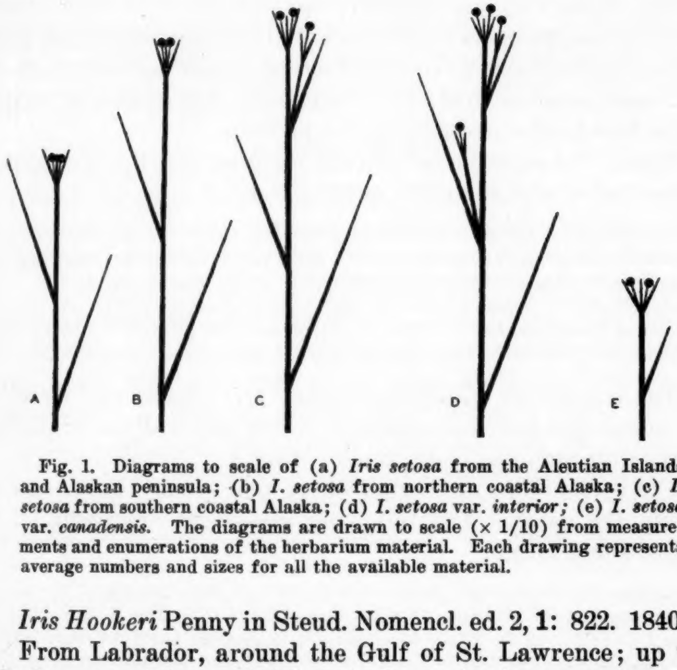


Fig. 1. Diagrams to scale of (a) *Iris setosa* from the Aleutian Islands and Alaskan peninsula; (b) *I. setosa* from northern coastal Alaska; (c) *I. setosa* from southern coastal Alaska; (d) *I. setosa* var. *interior;* (e) *I. setosa* var. *canadensis.* The diagrams are drawn to scale (× 1/10) from measurements and enumerations of the herbarium material. Each drawing represents average numbers and sizes for all the available material.

Iris Hookeri Penny in Steud. Nomencl. ed. 2, **1**: 822. 1840.

From Labrador, around the Gulf of St. Lawrence; up the St. Lawrence River to Riviere du Loup, Quebec, and along the coast to Washington Co., Maine.

This typical preglacial relict differs from the type only in its generally smaller size and lesser variability. As was pointed out by Dykes,[1] the smallest of the Alaskan specimens are indistinguishable morphologically from *I. setosa* var. *canadensis.*

[1] Dykes, W. R., The genus Iris. p. 94. 1913.

The averages of the plants of the two regions are strikingly different, however, as can be seen from fig. 1. Its greater conservatism (i.e. its lesser variability) is a general characteristic of the relict species and varieties around the Gulf of the St. Lawrence, as has been pointed out by Fernald.[2] This point is discussed at greater length in another section of the paper (see below, pp. 495–496).

Iris setosa var. interior

Iris setosa Pall. var. **interior**, var. nov.

Ab specie bracteis scariaceis vel crasse chartaceis non foliaceis rubicundiusculis saepe minoribus quam pedicellis differt.

Bracts scarious to thickly chartaceous, not foliaceous, somewhat florid, often exceeded by the pedicels.

Upper Yukon valley of Alaska, merging into the type in the lower valley and along the western coast.

Alaska: Fort Gibbon, frequent throughout the Yukon and Tanana valleys in lakes and along small streams, July 4, 1905, *Heideman 62* (US type); same locality, Aug. 10, 1905, *Heideman 98* (US); well-drained gully, Tolstoi, July 4, 1917, *Harrington 37* (US); Rampart, July 24, 1901 [fruit], *Jones 63* (US); alt. 150 m., vicinity of Fairbanks, Aug. 31, 1928 [fruit], *Mexia 2302* (MBG); Fairbanks, July 25, 1931, *Anderson 1221* (US); Fairbanks, June, 1927, *Palmer 1783* (US).

The characters which distinguish *Iris setosa* var. *interior* from the type have been found to characterize all the available herbarium material from interior Alaska. Transitional forms are to be found in the region where this great interior valley meets the coast. The following specimens represent such transitional forms:

Alaska: Ft. St. Michaels, Norton Sound, 1865–66, *Bannister s.n.* (US); moist grassy places, shade of alders, 16 miles west of Nome City, Aug. 5, 1900 [fruit], *Flett 1560* (US); on the Yukon River, between Andreafski and Anvik, July 16–18, 1889, *Russell s.n.* (US).

According to glacial geologists,[3] this large region remained unglaciated during the Pleistocene, and there, if anywhere, we

[2] Fernald, M. L. Persistence of plants in unglaciated areas of boreal America. Mem. Am. Acad. Arts & Sci. **15**: 244. 1925.

[3] Capps, S. R. Glaciation in Alaska. U. S. Dept. Inter., Geol. Surv. Prof. Paper 170–A. 1931.

might hope to find living irises most similar to those *Iris setosae* which must in preglacial times have extended across northern North America. A number of facts have been found which support this hypothesis and they are discussed below (p. 480).

While the irises of coastal Alaska are probably not varietally distinct from the type[4] (which is from Asia) there are minor geographical differences to be noted, when one compiles careful averages for such regions as the Arctic coast, the Alaskan peninsula and Aleutian Islands, and the southern Alaskan coast. Such averages have been prepared from all the available herbarium material and the results are presented graphically, to scale, in fig. 1, along with similar averages for *Iris setosa* var. *canadensis* and *Iris setosa* var. *interior.*

Iris versicolor

Iris versicolor L. Sp. Pl. ed. 1, 39. 1753.

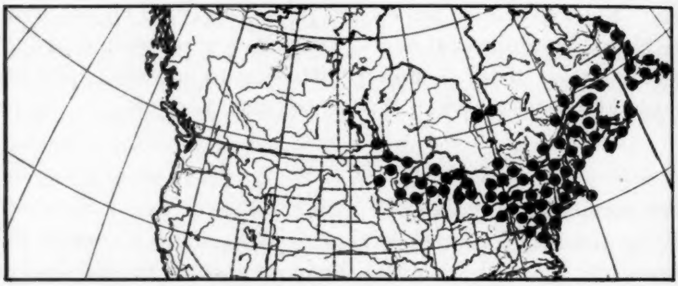
Perennial from a superficial or underground rhizome; rhizome stout, clothed with the fibrous remains of old leaves; leaves narrowly ensiform, 1–8 dm. long, 1–3 cm. wide, green to grayish-green; stem stout to slender, 2–6 dm. high, with one or two secondary branches, the latter *seldom equalling the main axis;* upper cauline leaves *seldom equalling the inflorescence;* inflorescence a compact, 2–4-flowered fascicle; bracts of the inflorescence thickly chartaceous to scarious, 3–6 cm. long, the margins *so heavily vernicose as to be much darker in color;* pedicels slender, some of those in each fascicle usually *longer than the subtending* bracts; sepals 4–7 cm. long, mostly *1.4 times the length of the petals* in living material; blade 2–4 cm. wide, variable in color in different plants, mostly violet-blue to blue-violet, the veins *slightly darker than the ground-color, minutely papillate at the base,* forming at most a dull greenish-yellow spot in living material; petals 2–5 cm. long, 0.5–2 cm. wide; ovary *1–2 cm. long in the flower, obscurely three-sided, slightly inflated at anthesis;* capsule short-cylindric, mostly symmetrical, somewhat verrucose without, *delicately vernicose*

[4] Hultén, Eric. Flora of Kamtchatka and the adjacent islands. Kungl. Svenska Vetenskapsakad. Handl. III. 5^1: 255–256. 1927.

within, usually persisting into the first winter; seeds D-shaped, often showing a *poorly developed raphe*, surface *regularly pitted, vernicose; chromosomes 106–108* (2n).

From Labrador to Winnipeg and southward to central Wisconsin, northeastern Ohio, and northern Virginia.

Morphologically, *Iris versicolor* is much closer to *Iris virginica* than to *Iris setosa*, though in every character by which it differs from *Iris virginica* it departs in the direction of *Iris*



Map 2. Range of *Iris versicolor*.

setosa. This peculiar intermediacy is discussed at length in the following section of this paper (pp. 478–480).

IRIS VIRGINICA

Iris virginica L. Sp. Pl. ed. 1, 39. 1753.

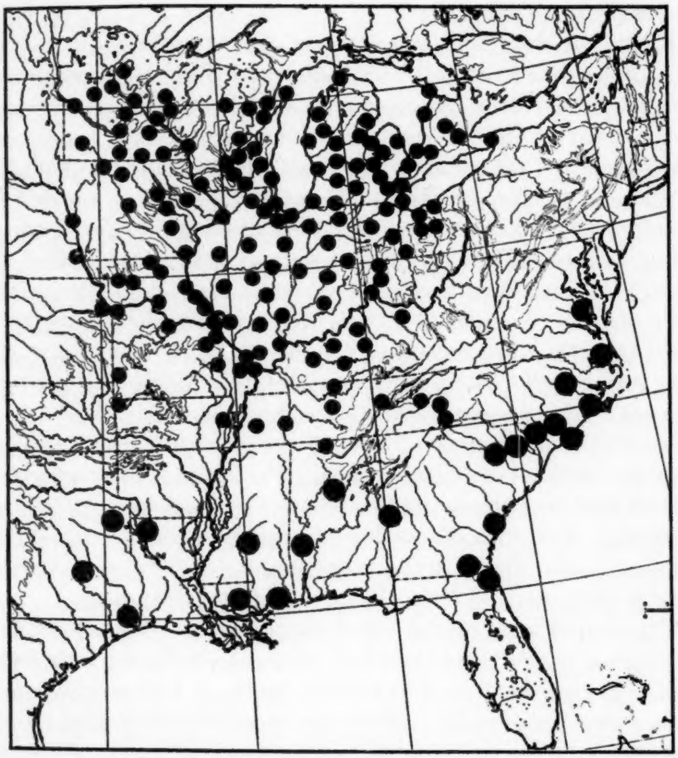
Iris carolina Radius, Naturforsch. Ges. Leipzig Schrift. 1: 158. *pl. 3.* 1822.

Iris caroliniana Wats. in Gray's Manual, ed. 6, 514. 1890.

Iris georgiana Britton, in Britton & Brown, Illust. Fl., ed. 2, 1: 537, *pl. 1330.* 1913.

Perennial from a superficial or underground rhizome; rhizome stout, clothed with the fibrous remains of old leaves; leaves ensiform, 2–9 dm. long, 1–6 cm. wide, green; stem stout, coarse, 3–10 dm. high, mostly with one secondary branch, the latter *usually subequal to the main axis;* upper cauline leaves *usually exceeding the inflorescence;* inflorescence a compact, 1–4-flowered fascicle; bracts of the inflorescence *coarsely* and

thickly chartaceous, 4–8 cm. long, *margins undifferentiated;* pedicels stout, *shorter than the bracts;* sepals 4–8 cm. long, mostly 1.2 times the length of the petals in living material; haft narrow with a *straight margin;* blade 1.5–4 cm. wide, blue to



Map 3. Range of *Iris virginica* (large circles), and of *I. virginica* var. *Shrevei* (small circles).

violet-blue and violet, veins *scarcely darker than the ground-color, thick pubescence of fine hairs* at base, forming a *bright yellow signal patch* in living specimens; petals 3–7 cm. long, 1–3 cm. wide; ovary *2–4 cm. long in the flower,* terete or obscurely three-sided, *not inflated;* capsule spherical to long-

cylindric, mostly *asymmetrical, suberose* and *coarsely verrucose* without, *never vernicose* within, seldom persisting until the seeds are fully ripe, valves of the capsule reflexed in well-ripened specimens; seeds *round* or D-shaped, *without a trace of a raphe,* surface *suberose, irregularly pitted; chromosomes 70–72* (2n).

From Virginia southward along the Atlantic coast.

Although well provided with distinguishing characteristics, *Iris versicolor* and *Iris virginica* seem to be under a special curse so far as their recognition in the herbarium is concerned. The shapes of the petals and sepals, the interior glandulosity of the calyx-tube and its shape—any one of these characters is sufficient for accurate specific delimitation. Unfortunately, *Iris virginica* differs also in texture and substance; its flowers, though larger, have less permanency. As a result they wilt very rapidly; even though carefully pressed when fresh, they have so little substance that the resulting specimens are too thin and fragile to be preserved intact. While the pressed flowers of *Iris versicolor* are none too accurate in their reflection of the original condition of the perianth, they are far superior to those of *Iris virginica.* The latter are so badly preserved that it is almost impossible to use them, even by boiling them up. Perianth dimensions from herbarium material are completely unreliable in these species, and for that reason have been largely omitted from the keys and descriptions.

The second most useful set of characters are those provided by the seed capsule and the seed. Here again the characteristic lack of permanency in the capsular walls of *Iris virginica* has been a great hindrance. With the exception of special collections made by the writer and by other recent students of American irises, herbarium specimens of *Iris virginica* seed capsules simply do not exist. The reason is not far to seek. The coarse stems of this species are neither durable nor stout, and they are not held above the leaves as in *Iris versicolor. Iris virginica* furthermore prefers slightly damper situations. In nature, therefore, the less lignified stems and seed-pods of *Iris virginica,* choked by iris leaves and other rank swamp vegeta-

tion, begin to rot long before the seeds are mature, particularly in the southern part of its range. By September it is not at all unusual to find the black, deliquescent, half-rotten seed-pods lying flat upon the ground, their corky brown seeds spilling out from the capsular remnants. A special collection of seeds and seed-pods has accordingly been brought together in the herbarium of the Missouri Botanical Garden as a permanent record, and the writer will be grateful for further material of either seeds or seed capsules, no matter how unattractive the partly decayed state of the latter.

It is unfortunate that mature capsular material is so difficult to obtain since it displays a curious and striking character, to which Small and Alexander[5] have called attention. The valves of the capsule in *Iris virginica* are strongly reflexed as in the related European species, *Iris pseudacorus* L.

Fortunately other characters can be found. Of these the most generally useful in the herbarium are the bracts of the inflorescence (the spathe-valves). Those of *Iris virginica* have the texture of coarse paper or thin cardboard. They may or may not be streaked with the fine chestnut lines caused by resinous deposits, but if so the streaking will be uniform throughout the bracts. In *Iris versicolor,* however, the bracts not only are of a finer, yet more durable texture, but the lignification is intensified towards the edge so that the margins are often deep chestnut and are distinctly vernicose.

In well-preserved specimens the pubescence at the base of the blade of the sepal is a useful character. In specimens of *Iris versicolor* it appears under the hand-lens as a minutely papillate area. In *Iris virginica* the hairs are larger, more overlapping, and are often conspicuously straw-colored.

In the field *Iris virginica* is readily identified by the larger, broader petals, the bright yellow pubescent spot on the sepal, and the spongy glandular inner surface of the calyx-tube with its sickish sweet fragrance.

Reasons for attaching the Linnean name *Iris virginica* to

[5] Small, J. K. and Alexander E. J. Botanical interpretation of the Iridaceous plants of the Gulf States. N. Y. Bot. Gard. Contr. 327: 356. 1931.

this species have been detailed elsewhere[6] and need not be repeated here, other than to state that the type is in existence and has been examined. The suggestion has since been made[7] that material from the presumable type locality may throw some doubt on this opinion. Through the kindness of Dr. T. W. Whitaker, I was able to obtain irises from Nesting, Gloucester County, Virginia, which is in the same general vicinity. Of these plants one or two answered the description given above; others showed signs of hybridization with *Iris versicolor* and were practically sterile. Reference to the distribution maps of *Iris versicolor* and *Iris virginica* (maps 2 and 3) will show that very region as the actual boundary zone of the two species. Because of this fact collections from or near the probable type locality are not so definitive as they otherwise might be.

Iris virginica is centered upon the Ozark-Appalachian landmass, an area which has been available for continuous plant occupancy since very ancient times. It would be strange indeed if no geographical differences were to be found within such a species, particularly in the case of the area along the Atlantic seaboard. Such differences are, however, rather difficult to find. At flowering time, I have been able to detect for the plants of the Atlantic seaboard only slightly narrower perianth segments, a larger average flower size (fig. 12), and an inflorescence which is characteristically somewhat less branched. The seed capsules, however, though variable, are distinct. Well-developed capsules from the upper Mississippi Valley are much longer than broad, while those from the coastal plain are practically spherical, as well as possessing larger, corkier seeds. Unfortunately the difficulty of collecting fruiting specimens of iris in the southern swamps (see above, pages 466–467) makes exact delimitation of the areas occupied by these capsular types a matter of the future. Throughout the upper Mississippi Valley and Great Lakes region it has been a comparatively simple matter to determine, and I am accordingly

[6] Anderson, Edgar. The problem of species in the northern blue flag, *Iris versicolor* L. and *Iris virginica* L. Ann. Mo. Bot. Gard. 15: 241–332. 1928.

[7] Small and Alexander. loc. cit. p. 356.

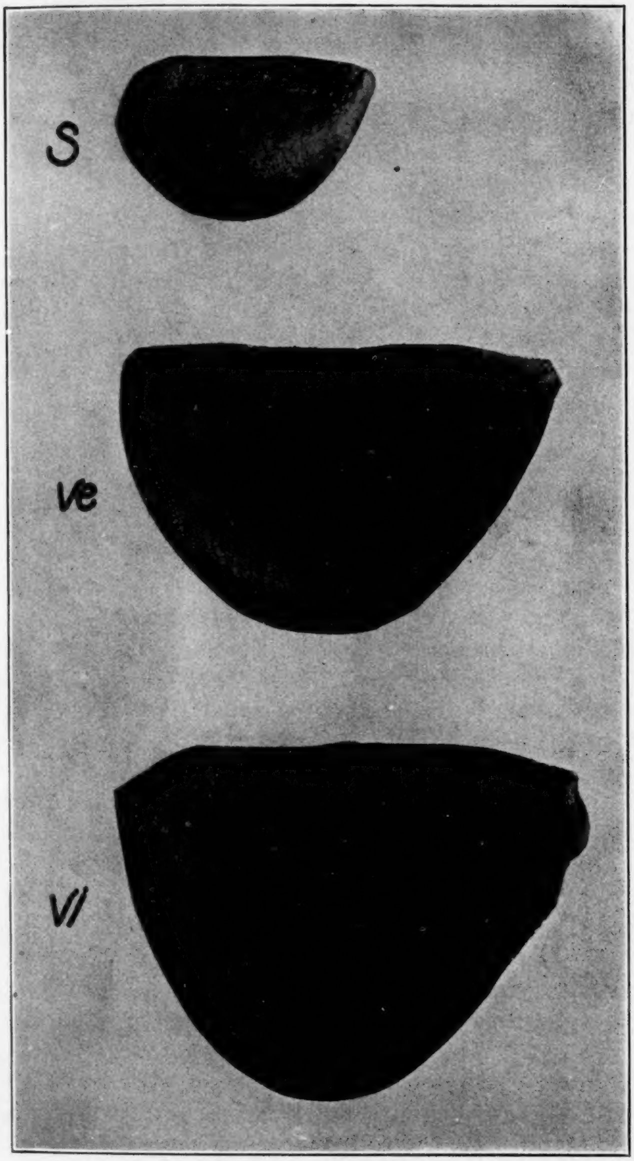
using Dr. Small's name *Iris Shrevei* in a varietal sense for these elongate-capsuled *Iris virginicae.* When adequate material is available for study it will be possible to determine the exact geographical relationships of this and probable other varieties of *Iris virginica.* Until such a time it has seemed prudent to recognize only this one variety, and to postpone for the present the precise delimitation of the typical and other possible varieties.

IRIS VIRGINICA VAR. SHREVEI

Iris virginica L. var. **Shrevei** (Small), comb. nov.

Iris Shrevei Small, Addisonia **12**: 13–14, *pl. 391.* 1927.

Mississippi Valley and Great Lakes region from southern Minnesota and southern Ontario, southwards to Texas and Alabama. The exact boundaries of its junction with the type as yet unknown and perhaps complex.



Seeds × 10: s, *Iris setosa;* ve, *I. versicolor;* vi, *I. virginica* var. *Shrevei.*

III. The Phylogenetic Relationship of Iris versicolor and Iris virginica

The northern blue flags, *Iris versicolor* and *Iris virginica,* were originally chosen for study because they were known to be closely related and preliminary investigation had shown that in any one locality they varied markedly from plant to plant. It was accordingly planned to study the minutae of variation so intensively in these two species that one might demonstrate the way in which one species had evolved from the other, or from some common ancestor. It seemed at the beginning of the work that here was splendid material for illustrating the way in which individual differences merge into racial, racial into varietal, and varietal into specific. A confident beginning was made with this end in view: five years of hard work showed that *Iris versicolor* might vary greatly and that *Iris virginica* might vary greatly but that each remained itself. They were of different fabrics. One might compare them to two old English villages, one in a sandstone region and the other in limestone. In each village there would be no two houses alike but all the houses in one village would be made of limestone, all those in the other made of sandstone. The conclusion was reached that closely related though these irises might be, variation within either species was of quite another order of magnitude from the hiatus between them (Anderson, '28). The variation *within* could never be compounded into the variation *between.* The two species were made of two different materials.

If one of these species was *not* derived from the other through the slow accumulation of minor differences, in what other manner could it have originated? Fortunately, at about the same time that these detailed studies of variation came to an *impasse* there were published a number of accounts dealing with another way in which species might originate in the higher plants: amphidiploidy. This phenomenon may well be illustrated by the case of *Primula kewensis* (Newton and Pellew, '29). *Primula kewensis* originated as a highly sterile hybrid between *P. floribunda* and *P. verticillata* (fig. 2). Kept alive by

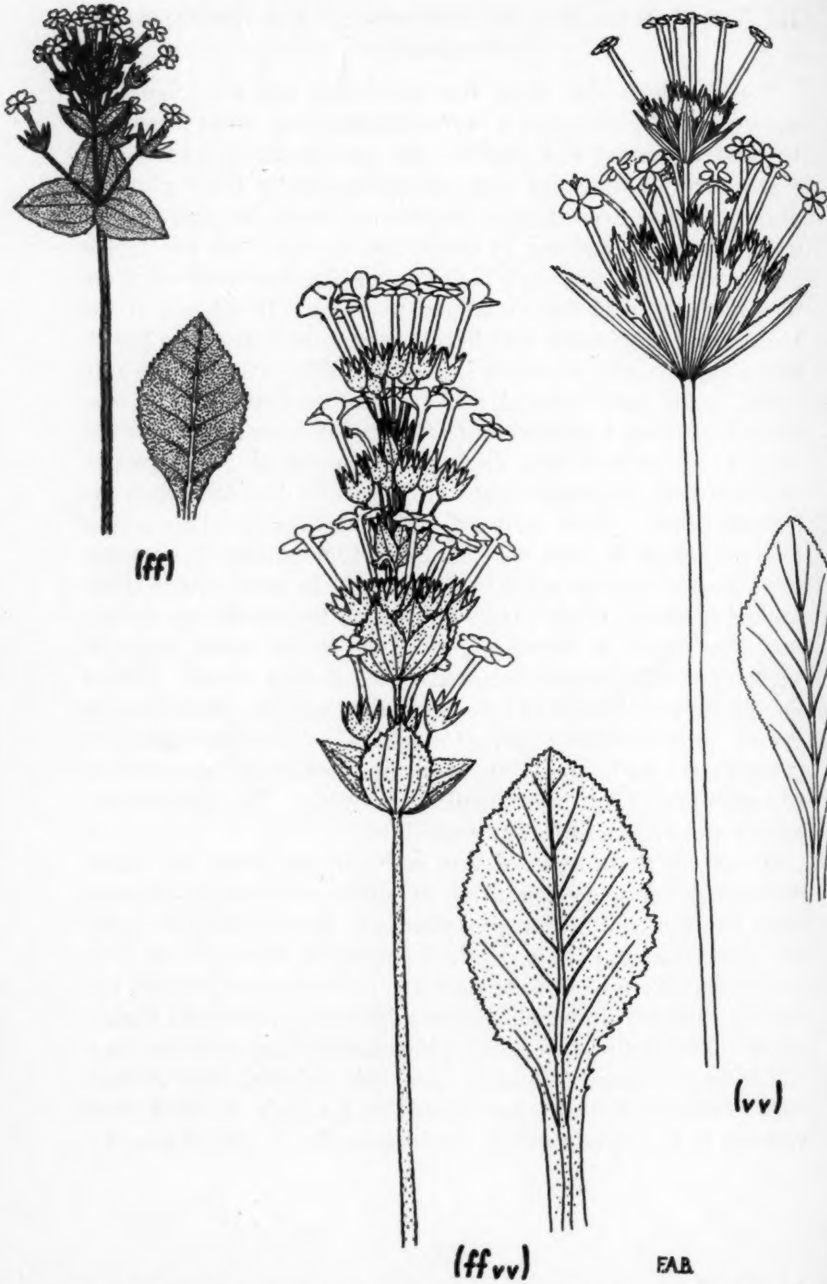


Fig. 2. *Primula floribunda* (ff), *P. verticillata* (vv), and their amphidiploid hybrid *P. kewensis* (ffvv). Drawn from herbarium specimens collected in the greenhouses of the John Innes Horticultural Institution.

vegetative reproduction, it has on several occasions produced fertile flowers. The progeny from these exceptional flowers have furthermore bred true, or substantially so, and the hybrids are today grown commercially by means of this fertile strain. Cytological examination has demonstrated that this fertile, true-breeding hybrid has 18 pairs of chromosomes, while the sterile hybrid and each of the parental species has 9 pairs. The fertile hybrid evidently originated when an exceptional nuclear division in the inflorescence of the sterile hybrid was not accompanied by a cell division and a sector arose in which the entire chromosome complement had been duplicated. On this hypothesis *Primula floribunda* might be diagrammed as 9F + 9F; *P. verticillata* as 9V + 9V; the sterile hybrid as 9V + 9F; and the fertile hybrid as 9V + 9V + 9F + 9F. The original hybrid was sterile because the two sets of chromosomes (V and F) were too unlike to pair and produce fertile gametes. Doubling the number resulted in two sets of V's and two sets of F's so that pairing could proceed regularly, producing a fertile, true-breeding hybrid, or amphidiploid.

Amphidiploidy, the production of fertile, true-breeding hybrids by doubling of the chromosome number, is now known to be a fairly common phenomenon among the higher plants (Winge, '32). It has occurred under controlled conditions in the experimental plots of many investigators. More than 24 such cases are now on record including several among floristically indigenous species (Müntzing, '30, '32; Clausen, '33). It has apparently occurred in the development of the cultivated irises (Randolph, '34). Amphidiploidy is largely confined to the flowering plants and is foremost among several factors which make specific relationships among the higher plants more intricate and more various than they are among the higher animals (Anderson, '31).

If our two blue flags did not originate by the slow accumulation of individual differences, the most likely explanation of their fundamental divergence is that one or both of them came into existence suddenly through amphidiploidy. A simple hypothesis immediately suggested itself.

Iris versicolor is geographically and morphologically intermediate between *Iris virginica* and the Arctic blue flag, *Iris setosa*. Might it be possible that *Iris versicolor* is an amphidiploid hybrid between these two species, a hybrid which occurred in pre-glacial or inter-glacial time? Startling as such an hypothesis seemed, it found confirmation in facts from such diverse fields as geographical distribution, cytology, morphology, and genetics. The hypothesis was used, with complete success, to predict the presence in central Alaska of a previously unrecognized variety of *Iris setosa*. It orients a number of facts which are either puzzling or meaningless on any other hypothesis. For all practical purposes it may be taken as proved though it is capable of still further tests.

The facts which support this hypothesis may be grouped under several different heads:

1. *Genetics*.—Although they have been placed in different sub-sections of the genus, *Iris virginica* and *Iris setosa* are at least partially fertile *inter se*. It is difficult in this latitude to bring both species into flower at the same time, but on one occasion it was possible to do so and two pollinations were made. From these two crosses of *Iris virginica* × *Iris setosa* were obtained two seed-pods well-filled with seeds, but with shrunken endosperms. None of them germinated, but it seems likely that if the cross could be repeated in quantity a few viable seeds could be obtained. It should be pointed out in passing that the most successful amphidiploids so far obtained have been between plants which are ordinarily quite sterile with one another. As was first pointed out by Darlington ('28, pp. 244–245), the more inter-sterile the two parents of an amphidiploid, the more fertile and true-breeding is the resulting progeny.

2. *Cytology*.—The cytological investigation has been hampered by the high chromosome numbers of *Iris virginica* and *Iris versicolor*, the highest known in the genus. This makes the determination of chromosome number and configuration rather difficult, and I am happy to report that my own counts have been completely confirmed by several other investigators,

principally by Randolph ('34). *Iris virginica* has 70 to 72 chromosomes [2n], *Iris setosa* has 38, and *Iris versicolor* has just what we would expect if it is an amphidiploid hybrid of the

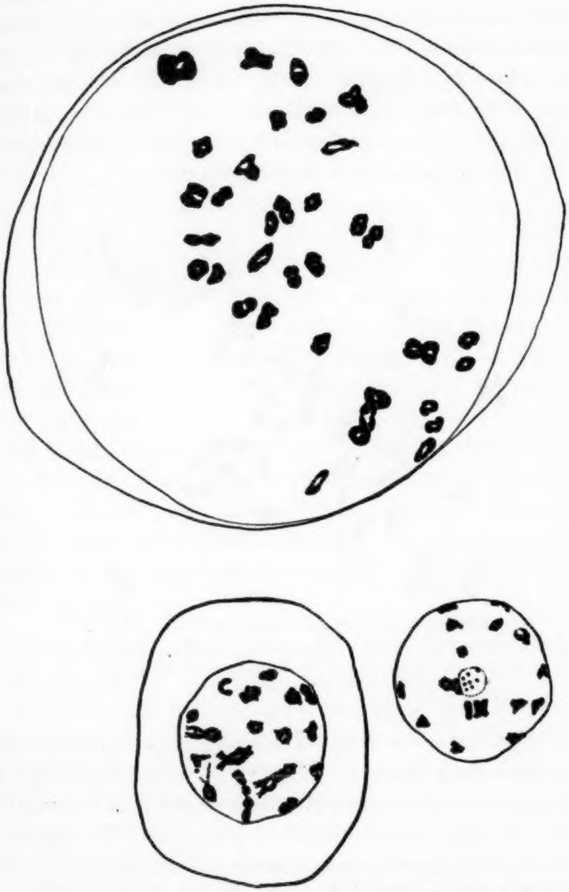


Fig. 3. Above: smear of early metaphase PMC. of *Iris virginica* var. *Shrevei* from Frankenmuth, Michigan, somewhat distorted by pressure. Camera-lucida drawing (made at bench level at × 2280, reduced to × 1140).

Below: smear of PMC. of *Iris virginica* var. *Shrevei* from Frankenmuth, Michigan. Late diakinesis, upper and lower hemispheres drawn separately.

two, 108 chromosomes. *Iris virginica* shows occasional multivalent association, mainly in fours, and very strong secondary association (fig. 3). These facts would suggest that it is itself an ancient amphidiploid hybrid of two species each with 36± chromosomes. *Iris versicolor* has occasional multivalents; hexavalents such as the one illustrated in fig. 4 are not uncommon. The cytological facts therefore are in complete agreement with our hypothesis, and they go even farther by suggesting that *Iris virginica* is a set of two genoms and *Iris versicolor* the component of three genoms.

Fig. 4. Aceto-carmine smear of PMC. of *Iris versicolor* from Connecticut Lakes, N. H. Camera-lucida drawing (made at bench level × 2280, reduced to × 1140).

3. *Geographical evidence.*—The three species of irises which we are considering have strikingly different distributions in North America, and the distribution of each is characteristic of many of the plants with which it is found. The significance of these areas has been pointed out by Fernald ('31). Of the region about which the *Iris virginica* is centered he says: "Temperate eastern North America has, then, an extensive area (the southern Appalachian Upland) in which land-plants have had an opportunity to spread since the advent of the Angiosperms."

The other putative parent species, *Iris setosa,* also comes from a region (again we quote Fernald) "which apparently retained [its] present distinctive flora through at least the last glaciation."

Iris versicolor, which we are presuming to derive from these two ancient species, inhabits a more youthful region, one characterized by Fernald (loc. cit., p. 28) as "the vast region of Canada and the Northern States which has become available for wholesale occupation by plants only since the decay of the Wisconsin ice, within the last few thousand years."

The geographical facts, therefore, point to *Iris virginica* as an ancient southern species and to *Iris setosa* and its variety *canadensis* as being certainly pre-glacial. *Iris versicolor,* our putative hybrid, is either late pre-glacial or inter-glacial. The present distributions of the species would suggest that the original hybridization (or hybridizations) took place in the interior of the continent, perhaps in the general region of the present-day Great Lakes. As will be shown below there are morphological reasons for believing that the *Iris setosa* which entered into the cross was not the depauperate remnant which lingered on around the Gulf of St. Lawrence. The actual ancestor is rather to be sought among the hordes of *Iris setosa* which must have occupied the interior of the continent before the glacial period.

4. *Habitat.*—In its habitat preferences *Iris versicolor* is likewise intermediate. It grows in situations more moist than those preferred by *Iris setosa* and a little drier than those in which *Iris virginica* is found. The three species are not found growing together in nature at the present time but *Iris versicolor* is found with each of the others. Around the Gulf of St. Lawrence the marked preference of *Iris setosa* var. *canadensis* for drier situations has been noted by a number of investigators. In Michigan and Ontario, where *Iris versicolor* and *Iris virginica* are growing together, it can be seen that *Iris versicolor* will continue to flower and fruit in spots so dry that *Iris virginica* only persists vegetatively. It is not uncommon to find *Iris virginica* growing luxuriantly in marshes where

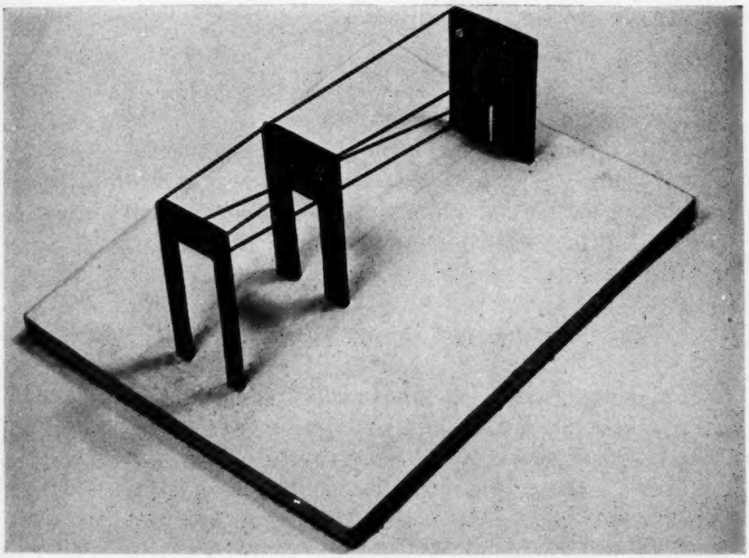
there is standing water over its roots for several months during the growing season. *Iris versicolor* may tolerate such a situation but does not welcome it.

5. *Morphology.*—Before considering these data in detail it may be well to point out again that, according to our hypothesis, *Iris versicolor* was formed by the summation of *Iris setosa* with 38 chromosomes and *Iris virginica* with 70. In other words it received two doses of *Iris virginica* but only one of *Iris setosa.* We should expect therefore to find *Iris versicolor* in an intermediate position morphologically but much closer to *Iris virginica* than to *Iris setosa.* Such does actually prove to be the case.

Fig. 5. Outline drawings of petal and sepal from plants of *Iris setosa* (left), *I. versicolor* (center), and *I. virginica* var. *Shrevei* (right).

In the living plant the size and dimensions of the petals and sepals are among the best diagnostic characters for these three species (as indeed for most species of *Iris.*) It will be seen that *Iris setosa* differs from *Iris virginica* in having a shorter, broader sepal and a much smaller and narrower petal. *Iris versicolor,* as our hypothesis demands, has differences in this direction. These significant dimensions are presented diagrammatically in fig. 5. These differences in proportion of sepal and petal are so absolutely in accord with the theoretical demands that, given any two of the three species, it is possible to derive the average proportions of the other by statistical prediction. (pl. 23).

The sepals of *Iris virginica* bear a bright yellow pubescent patch, the hairs of which are clearly visible to the naked eye. No such patch exists in *Iris setosa,* and the epidermal cells are



Photograph of three-dimensional model showing the precise geometrical relationship in petal and sepal size and proportions of *Iris virginica* (left), *I. versicolor* (center), and *I. setosa* (right). In the model, *Iris versicolor* is placed two-thirds of the distance between the two putative parents, since their chromosomal contributions to the hybrid are in the approximate ratio of 2 to 1. Measurements combined by method illustrated in figure 8.

seen to be barely papillate when examined with a strong hand-lens. *Iris versicolor* is intermediate; the bearding is clearly visible only with a hand-lens and the color is at best a kind of greenish-yellow. The blade of the sepal in *Iris setosa* is broad and slightly undulate, in *Iris virginica* it is narrow and straight; *Iris versicolor* presents an intermediate condition.

The ovary of *Iris setosa* inflates rapidly after fertilization so that in the ripening capsule there is a wide space between the walls and the seeds. In *Iris virginica* the walls are stretched tightly over the seeds, in *Iris versicolor* the condition is intermediate though nearer to that of *Iris virginica.*

In *Iris setosa* the capsules and stem are so strongly lignified that they sometimes persist for over two years, and it is customary to find last year's seed stalks among this year's flowers. In *Iris virginica* the capsule and stem, though much larger, are poorly lignified. In the humid swamps of the south they fall over and the capsule usually is more or less disintegrated by the time the seed is ripe. Here again *Iris versicolor* is intermediate; the capsules usually persist well into the winter but are seldom found the second season.

Iris setosa bears seeds which are unique in the genus. They are small, heavily vernicose, and with a conspicuous raphe down one side. *Iris virginica* bears large, spongy seeds which may be either round or D-shaped. When the above working hypothesis was first considered, one possible objection seemed to be the fact that *Iris versicolor* was without a raphe. Subsequent examination of the seeds of *Iris versicolor* shows that it does have the shadow of one on nearly every seed and had even been illustrated as having one (though without comment) in Dykes' plate of *Iris* seeds in his monograph of the genus ('13). (See pl. 22.)

When minute comparisons were made in this way, character by character it was found that there were, however, at least three characters in which *Iris versicolor* was not intermediate between *Iris virginica* and *Iris setosa* var. *canadensis.* The theory demanded an *Iris setosa* with several flowering branches, with pedicels longer than the bracts, and with bracts not greenish but brown and subscarious. Since the demands of

the theory were met so minutely on all the other characters it seemed possible that these three represented details in which the race of *Iris setosa* entering into the original hybridization differed from *Iris setosa* var. *canadensis*. Such a race might conceivably have present-day relatives living among the *Iris setosa* which is so widely spread in Alaska and Asia, since the species is notoriously variable there. Herbarium material was accordingly consulted. The first few specimens examined proved most disappointing. They were from localities along the arctic coast and they had none of the three desired qualities. Their bracts were long and green, completely eclipsing the pedicels, and the plants were unbranched. Farther down in the pile, however, was a plant which had not only long pedicels, but scarious bracts and a branched inflorescence, the very combination desired. Farther on was another and eight specimens in all were found.

When their distribution was plotted it was found that all came from central interior Alaska and represented, in fact, the only specimens from that region. They have accordingly been described above in the taxonomic section of these papers as a new variety, *Iris setosa* var. *interior*.

Further search unearthed the even more significant fact that *Iris setosa* var. *interior* grows in that part of Alaska which was adjacent to the edge of the continental ice-sheet (map 1). If representatives of the pre-glacial races of *Iris setosa* which must once have covered much of northern Canada are to be sought anywhere today, glacial geologists would suggest this very region (Capps, '31). In other words, we not only found the variety demanded by the theory but we found it in exactly the region which the theory would suggest as most likely.

The comparison of the three species can be closed therefore with the presentation of diagrams to scale of *Iris virginica*, *Iris versicolor*, and *Iris setosa* var. *interior*. It will be seen that in size, node number, leaf length, number of branches, length of pedicels, and length of bracts the demands of the hypothesis are exactly met (fig. 6).

Though it is capable of still more rigorous tests, the theory that *Iris versicolor* is a pre-glacial, or inter-glacial, amphi-

diploid hybrid between *Iris virginica* and *Iris setosa* var. *interior* would seem to be well established as a working hypothesis. Ultimately it should be possible, as in the case of the European *Galeopsis Tetrahit* (Müntzing, '30), to re-synthesize the species from its two constituents.

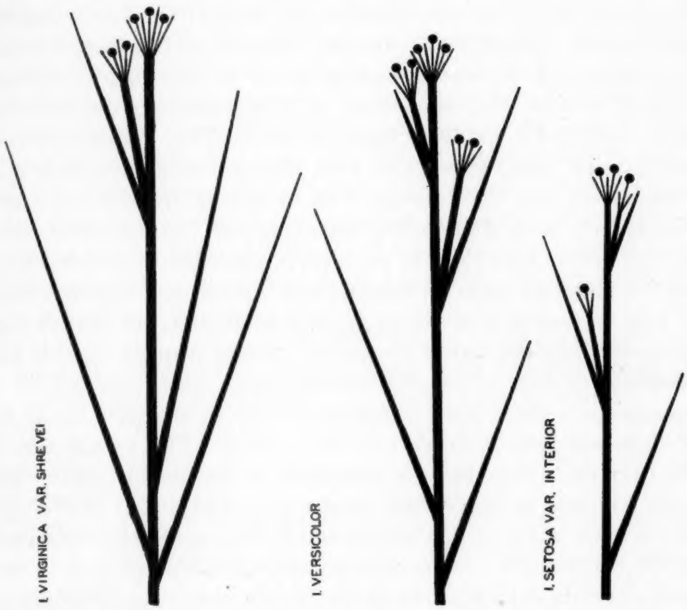


Fig. 6. Diagrams to scale of *Iris setosa* var. *interior*, *I. versicolor*, and *I. virginica* var. *Shrevei*. The diagrams represent precise averages of all the available herbarium material.

The hypothesis also gives an explanation to several curious facts which had previously been most puzzling. The first might be called the one-way relationship between *Iris virginica* and *Iris versicolor*, or so I have attempted to phrase an impression received from long-continued study of variation within these two species. It seemed that the relation of *Iris versicolor* to *Iris virginica* was quite different from that of *Iris virginica* to *Iris versicolor*, or to state it somewhat less mystically, that *Iris versicolor* often reminded one of *Iris virginica*, but *Iris vir-*

ginica never reminded one of *Iris versicolor.* If on the above hypothesis *Iris versicolor* is indeed *Iris virginica* plus something else, then the relationship should be different in one direction from what it is in the other.

Another puzzling fact had been the frequency of albinos. *Iris virginica* and *Iris versicolor* by any ordinary standard were unusually variable species yet pure albinos were exceedingly rare. In spite of prolonged search and inquiry I found only three in *Iris virginica* while in *Iris versicolor* I have found no pure albino without a trace of blue, and only one case has been reported in the literature (Fernald, '36). Yet albinos are common in many species of *Iris,* as, for instance in *Iris missouriensis;* why then should they be absent from our common blue flags? Why should they shun this particular species which by any other standard is peculiarly variable in flower color? On the above hypothesis this is exactly what one might predict. If *Iris virginica* is made up by the summation of two ancient species, albinism, being recessive, cannot appear until it has occurred in each of the constituent sets. In *Iris versicolor* it cannot show itself until it appears in these and also in the set of chromosomes derived from *Iris setosa.* This means that if the original frequency of albinism in the basic species had been, say one in every 5000, that we should find it in *Iris virginica* once in every 25,000,000 and in *Iris versicolor* only once in 125,000,000,000. The infrequency of albinism in *Iris virginica* and its even greater rarity in *Iris versicolor* is therefore in strict accord with theoretical expectations.

SUMMARY

1. The absolute morphological discontinuity previously discovered between the closely related *Iris versicolor* and *Iris virginica* is explained by the following hypothesis: *Iris versicolor* originated suddenly as a fertile, true-breeding hybrid (an amphidiploid) between the southern *Iris virginica* and the subarctic *Iris setosa,* in pre-glacial or inter-glacial times.

2. Since the former has 70 chromosomes and the latter 38 we should expect to find *Iris versicolor* generally intermediate be-

tween these species though much closer to *Iris virginica.* This is found to be the case.

3. A consideration of one or two minor exceptions to this generalization led to the discovery of a previously unrecognized variety from central Alaska, *Iris setosa* var. *interior.*

4. Since it harmonizes so many otherwise incoherent facts from cytology, morphology, geographical distribution, genetics, and geology, the theory is taken to be well established as a working hypothesis.

5. The theory also explains two phenomena which had previously seemed incomprehensible: (1) the "one-way" morphological relationship between *Iris virginica* and *Iris versicolor,* (2) the infrequency of albinos in *Iris virginica* and their even greater rarity in *Iris versicolor,* a species otherwise unusually variable in flower color. It is shown that both of these results are to be expected on the basis of the above hypothesis.

BIBLIOGRAPHY

Anderson, Edgar ('28). The problem of species in the northern blue flags, *Iris versicolor* L. and *Iris virginica* L. Ann. Mo. Bot. Gard. **15**: 241–332.

————, ('31). Internal factors affecting discontinuity between species. Am. Nat. **65**: 144–148.

Capps, S. R. ('31). Glaciation in Alaska. U. S. Dept. Inter. Geol. Surv. Prof. Paper 170-A.

Clausen, J. ('33). Cytological evidence for the hybrid origin of *Pentstemon neotericus* Keck. Heriditas **18**: 65–76.

Darlington, C. D. ('28). Studies in Prunus, I and II. Jour. Gen. **19**: 213–256. *pl. 11–18.*

Dykes, W. R. ('13). The genus Iris.

Fernald, M. L. ('31). Specific segregations and identities in some floras of eastern North America and the Old World. Rhodora **33**: 25–63.

————, ('36). Albino *Iris versicolor. Ibid.* **38**: 52.

Müntzing, A. ('30). Outlines to a genetic monograph of the genus Galeopsis. Hereditas **13**: 185–341.

————, ('32). Cyto-genetic investigations on synthetic *Galeopsis Tetrahit. Ibid.* **16**: 105–154.

Newton, W. C. F., and C. Pellew ('29). *Primula kewensis* and its derivatives. Jour. Gen. **20**: 405–467.

Randolph, L. F. ('34). Chromosome numbers in native American and introduced species and cultivated varieties of Iris. Am. Iris Soc. Bull. 52: 61–66.

Winge, Ö. ('32). On the origin of constant species-hybrids. Svensk Bot. Tidskr. **62**: 107–122.

IV. Intra-specific Differentiation in the Northern Blue Flags

As has been related in the previous paper of this series, detailed studies of variation were made in two species of *Iris* with the aim of demonstrating the way in which one had arisen from the other. Though they failed to produce any such evidence (and have as a matter of fact led to a very different hypothesis of the phylogenetic relationship between these two particular species), the data may still be used to examine the way in which evolution has proceeded and is proceeding to build up differences within these species. Many of the actual data have been presented in full in a previous communication (Anderson, '28). Since that time, however, the interpretation of this evidence has been profoundly affected by information derived from other fields of study.

The following paper is largely concerned with the results of a detailed morphological census of two species of *Iris* in eastern North America, *I. versicolor* and *I. virginica;* some attention has also been paid to the related glacial relict, *Iris setosa* var. *canadensis.* The results of such a census may be presented individual by individual or they may be grouped and averaged in various ways. In the following census the colony is recognized as a vegetational and evolutionary unit of major importance, so far as irises are concerned. Throughout most of the region in which they are found today, *I. versicolor* and *I. virginica* grow in small colonies of from one to several thousand individuals. Single individuals usually cover several square feet and send up several flowering stalks each year. In exceptional cases one individual may by vegetative reproduction cover a much larger area, and in rare instances a colony of several acres may be composed genetically of but one plant.

With a little study the recognition of individual plants is not at all difficult. The sea of blue-purple flowers which at first glance seems so uniform resolves itself into a little community with quite as much divergence between the various members as is found in human communities. One plant will have brown spots on the sepals of each flower, the next one will be without

the spots but will claim attention by the extraordinary size of its petals. Another will have flowers which are a very light blue, still another will have flowers which are almost wine colored, another will have deep notches in the petals. And just as in a village each man has a hand with characteristically different proportions from all other men yet has his left and right hands built on almost the same pattern, so it is in a swamp full of irises. The petals and sepals of the different flowers on a plant will have substantially the same proportions, but these proportions will vary tremendously from plant to plant. This point is illustrated in pl. 24 where three flowers are shown from each of six plants. These photographs were taken with identical illumination and exposure and were developed and printed uniformly. The differences in shade are due to differences in the flowers themselves; plant no. 2 had flowers of a very light blue and they have photographed almost white; plant no 6 had a great deal of red in with the blue and it is much darker in the picture. It will be noticed that even such a tenuous character as the carriage of the petals and sepals is based upon inherent factors; note, for instance, the floppy aspect of all three flowers of no 5, the contrasted horizontal sepals and upright petals of no. 1, the undulate sepal margins of no. 3.

The number of such colonies is enormous; a rough approximation has been made by observing the numbers to be seen from the highway along various routes and converting these figures into number of colonies per square mile. The method seems to be reasonably accurate, since it yields consistent results when different trips are made through the same territory. According to this method, the average frequency of *Iris* colonies per 100 square miles is 120 in northern Michigan, 350 in southern Michigan, 170 in northern Illinois, 30 in southern Missouri, and 5 in Alabama and Mississippi. Colonies are particularly frequent north of the terminal moraine where an uneven glacial topography produces many small swampy areas favorable for the growth of *Iris*. Figure 7 illustrates a representative area of 50 square miles within this region. It

Three flowers each from six plants of *Iris virginica* var. *Shrevei* from Portage des Sioux, Missouri.

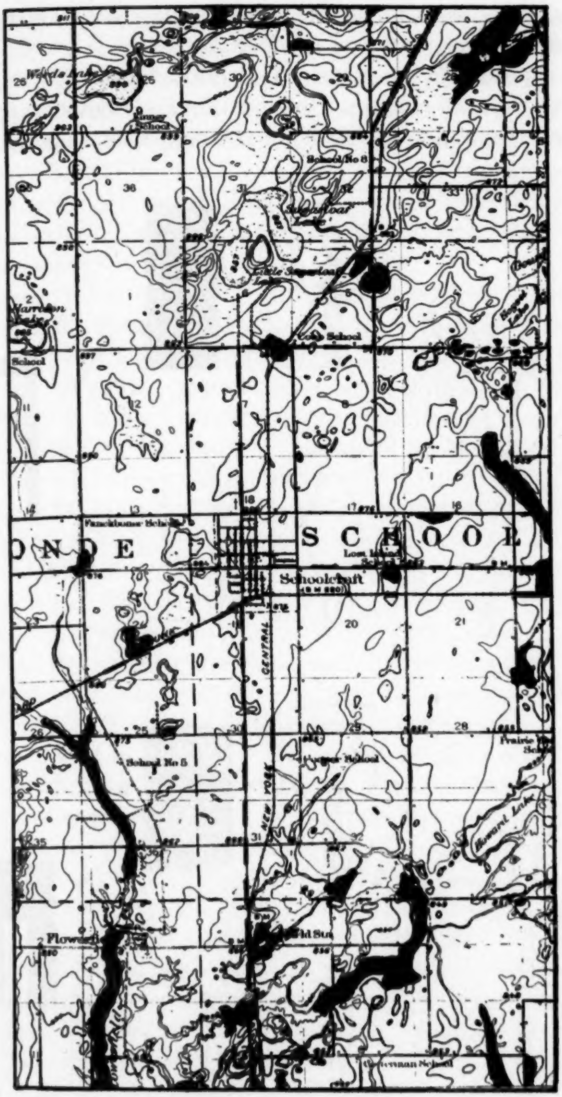


Fig. 7. Representative region of 50 square miles in southern Michigan. Areas occupied by *Iris virginica* var. *Shrevei* shown in solid black.

demonstrates how numerous are the *Iris* colonies and how isolated they are from one another.

It is a point of some theoretical importance (see below, pp. 495–496) that the colonies are probably distributed in much the same way that they were before the land was cleared but that

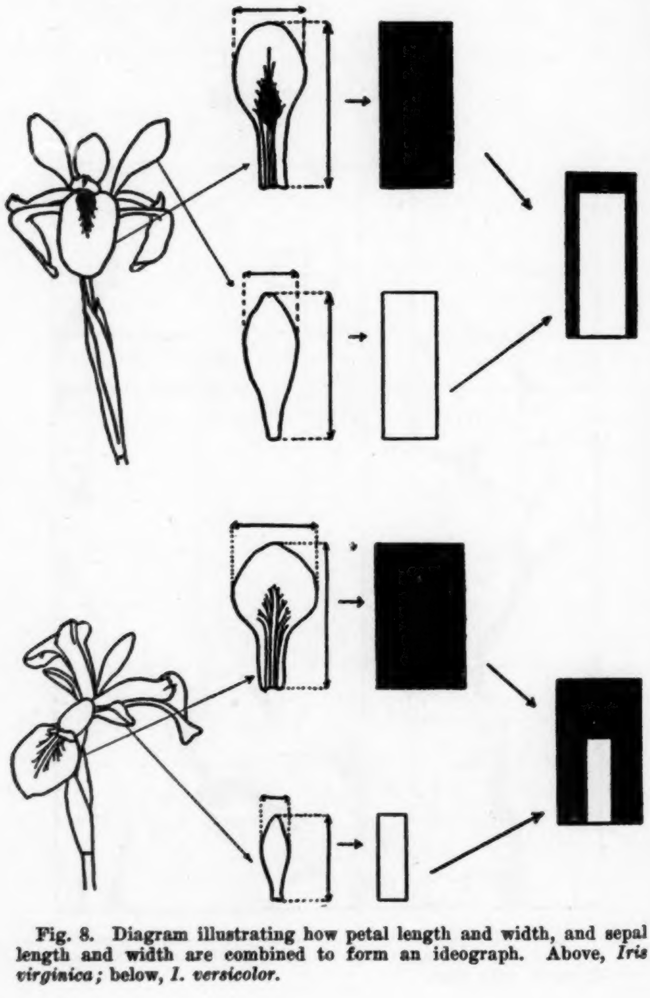


Fig. 8. Diagram illustrating how petal length and width, and sepal length and width are combined to form an ideograph. Above, *Iris virginica;* below, *I. versicolor.*

the numbers of individuals in the colonies are greater. The deforestation and pasturing of swampy areas have increased many fold the area available for these irises throughout the northern states. Turning the land over to pasture is particularly helpful to them since grass, their worst competitor, is kept down by the livestock. In most cases large colonies now numbering thousands of plants are probably the descendants of a much smaller number which were growing in that area before the land was cleared.

The census has to do with four measurements; length and width of sepal, length and width of petal. Since such measurements are of greatest significance when their interrelations with each other are understood, the results are presented graphically in a way which makes it possible to convey these relationships simultaneously. Figure 8 shows how the four measurements of each flower can be built up into a simple black-and-white diagram. This diagram or "ideograph" is essentially a white petal superposed upon a diagrammatic black sepal. Figure 9 presents ideographs for 20 plants of *Iris versicolor* and 20 of *Iris setosa* var. *canadensis* which were growing together in a pasture near Île Verte, Quebec (Anderson, '35). It demonstrates how such ideographs may be used to present a large amount of data in a small space. Figure 9 is a graphical summary of four measurements and six proportions on each of 40 plants. It is, in other words, a simultaneous presentation of 400 separate facts. The precise comparison of such colonies can be carried farther by the production of *average* ideographs for the whole colony, utilizing the average petal length, the average petal width, the average sepal length, and average sepal width (fig. 9, central ideographs).

The data for colonies are presented in this way in figs. 10 and 11. The colonies are arranged by species and subspecies and within these categories are placed roughly according to geographical position from south to north. A study of these figures yields the following conclusions:

1. There is little or no regional differentiation in shape within any of the subspecies. No general characteristics can be recognized for the irises from southern Michigan or from

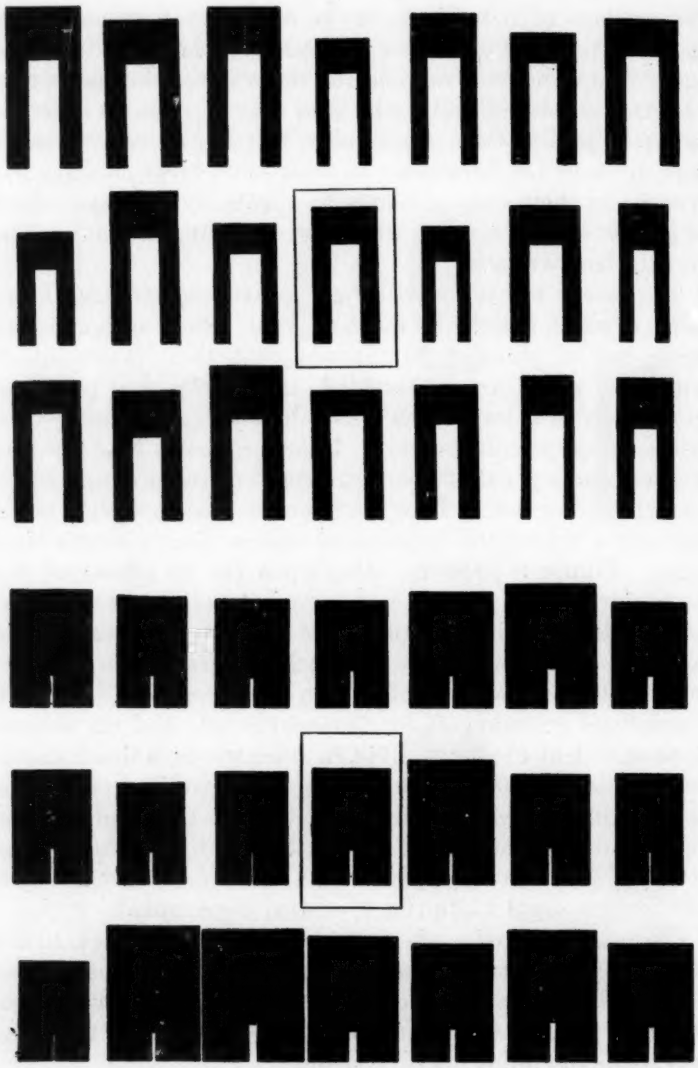


Fig. 9. Ideographs of 20 plants of *Iris versicolor* and 20 of *I. setosa* var. *canadensis* from Ile Verte, Quebec. Averages of entire colony (50 for each species) shown in central frames.

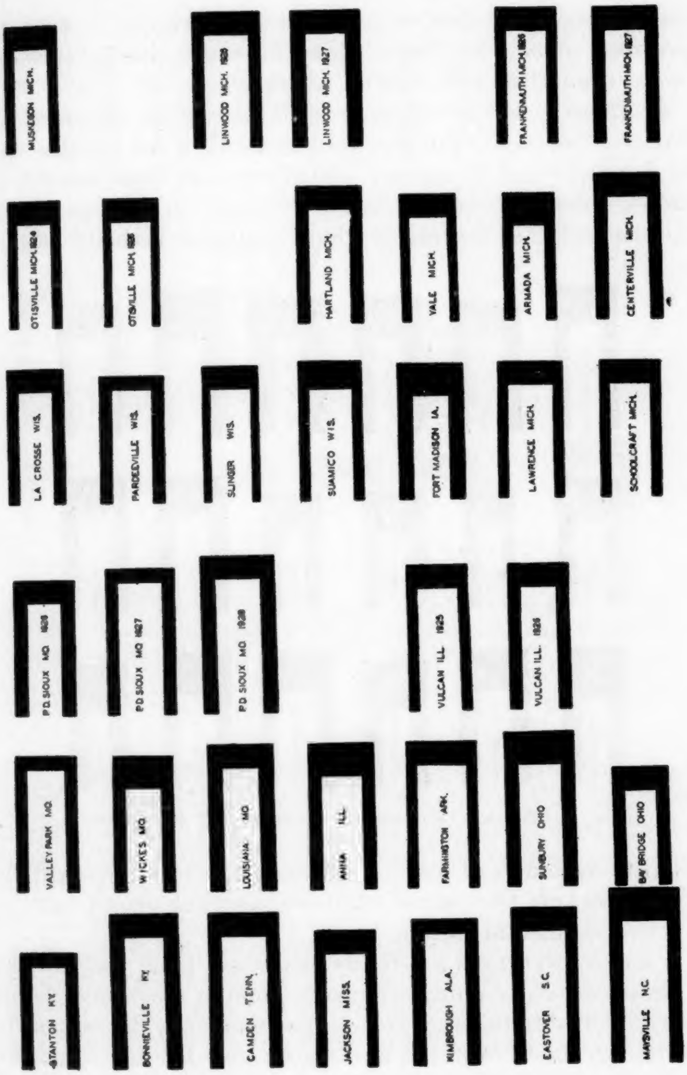


Fig. 10. Average ideographs for 31 colonies of *Iris virginica* and *I. virginica* var. *Shrevei.*

the Mississippi Valley, or from the Cumberlands, or from the prairies. As will be shown below, this conclusion is reinforced by the computation of *regional* averages.

2. There is a very slight trend in size. *Iris virginica* var. *Shrevei* reaches its greatest development in the Cumberlands of Kentucky and Tennessee. Northward or southward it becomes somewhat smaller on the average. *Iris versicolor,* on the contrary, is largest in the north and becomes smaller

Fig. 11. Average ideographs for 18 colonies of *Iris versicolor.*

towards its southern limits. Transplants from these various areas have kept their same relative sizes when grown together in the experimental garden.

3. Colony averages are fairly consistent from year to year in those cases where measurements could be made in different years. Allied to this fact is the experimental evidence that the flowers of plants collected and grown together in the garden maintained their characteristic size, shape, color, and color pattern. In several cases divisions of the same plant have been grown and studied in Boston, St. Louis, and Schoolcraft,

Michigan. For these reasons the differences which distinguish the individual plants and thereby create the peculiarities of the colonies are thought to be largely inherent. An even stronger proof is the fact that progeny tests of several individuals produced evidence for the heritability of various individual peculiarities.

4. There are striking differences between colony averages, even for the same region. The colony averages of figs. 10 and

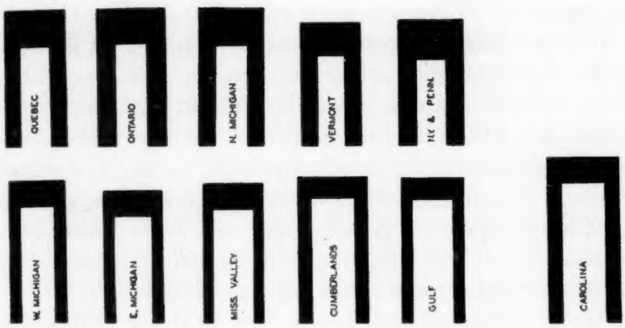


Fig. 12. Regional averages for *Iris versicolor* (above), *I. virginica* var. *Shrevei* (below, left) and *I. virginica* (below, right).

11 are particularly instructive when compared with the regional averages of fig. 12. It will be noted that though there are differences between the regions they are slight, and they have no evident geographical trend other than the slight one in size already referred to. The regional differences are indeed so slight that the variation in these irises might seem to be without any phylogenetic significance. If attention is shifted from the regions to the colonies, the evolutionary significance of the variation is more manifest. Each little colony is a more or less independent evolutionary unit and has evolved a more or less distinctive combination of characters. All that is necessary for the production of a regional variety is the isolation of any *one* of these colonies. Were some succession of droughts and floods to exterminate the great bulk of either species, leaving only two or three colonies persisting in different parts of

its present range, and were the area to be repopulated from these centers we should then have the formation of geographical varieties. The majority of the colonies as they exist at the present have achieved sufficient individuality to be rated as incipient varieties were they only to reproduce their several types over larger areas. For an actual difference of this magnitude we may compare *Iris virginica* of the Atlantic seaboard and *Iris virginica* var. *Shrevei* of the Mississippi Valley. For an inconceivably long time the irises of the seaboard have been somewhat isolated from their relatives in the Mississippi Valley. It is not surprising then that though we can find no outstanding differences in sepal and petal proportion within the interior of the continent, there is a slight difference between the irises from the interior and those from the seaboard. *Iris virginica* has flowers which are distinctly larger and somewhat narrower. The difference is a minor one as compared to the distinct hiatus between *I. versicolor* and *I. virginica,* but it is reinforced when we study such technical characters as the shape of the seed capsules and the size of the seed.

Particularly significant is the fact that the difference between *I. virginica* and *I. virginica* var. *Shrevei* is of about the same order of magnitude as the differences between colonies of *I. virginica* var. *Shrevei.* It would indeed be possible to find two swamps in the same township in southern Michigan whose iris populations have as great an average difference as that between *Iris virginica* of the Atlantic Coastal plain and *Iris virginica* var. *Shrevei.* But in this latter case the difference, slight though it is, characterizes a whole region and has superimposed upon it the varying pattern of colony differences in each region.

An evolutionary factor of basic importance in our common blue flags, therefore, is the rapid accumulation of minor differences in the little colonies into which the species are divided. Nearly every colony carries within itself the potentialities of a variety or a subspecies. The conditions under which these irises exist seldom release these potentialities. Many colonies arise, develop a distinctive type, and pass on with little or no influence on the main evolutionary stream. It should be re-

membered that the territory in which they are growing possesses very few geographical or climatic barriers. But the potentiality is there and when opportunity allows a colony to play a larger role it is ready to do so. Then the peculiarities evolved in one colony, or a few colonies, might come to characterize all the colonies of a region.

By mathematical deduction from the known facts of genetics, Wright ('31) has produced a generalized theory of evolution. From the standpoint of pure theory he finds that evolution will proceed most effectively neither in a large inter-breeding population nor in a very small one but in a large population "divided and sub-divided into partially isolated local races of small size." Under such conditions he predicts "a continually shifting differentiation among the latter which inevitably brings about an indefinitely continuing, irreversible, adaptive, and much more rapid evolution of the species."

The irises of this study present just such a picture. They are divided into partially isolated small colonies ["Local races"] which before the land was cleared were probably even smaller. These colonies differ from one another and from the mean of the species to a degree which is almost of varietal magnitude. Their differences are inherent and to all appearances are largely non-adaptive. Isolation, in dividing the species up into these smaller units, has made possible their several divergencies. Were isolation to be made complete, as by another glacial period, the phylogenetic potentialities of the survivors would be released and what had been colonial peculiarities might become varietal differences.

The variation within *Iris setosa* var. *canadensis* seems particularly instructive in the light of its recent history. It is typical of those species whose once continuous range across northern North America was reduced to the northeastern and northwestern edges of the continent by the Pleistocene ice. In Alaska a large central region was left unglaciated; around the Gulf of St. Lawrence, on the other hand, the plant refuges in glacial times were little more than rocky nunatacks rising above the ice. The results on the two sets of irises are just what a geneticist might predict. Even from the few specimens

which are available in herbaria one can see that the *Iris setosae* of Alaska are a varied assemblage. They include one well-marked variety (described above) and several fairly well-marked regional variants. The irises of eastern Canada present a very different picture. Figure 9 gives some slight indication of their lesser variability from plant to plant. Compared to the millions of irises which might well have continued to live in Alaska during the ice age, those of the St. Lawrence region were a mere handful. From that handful must have descended the millions upon millions of irises which now carpet the meadows and shores of that region in early summer (Anderson, '35). Compared with our other American blue flags they are a singularly invariable lot. Graphical comparisons are made in fig. 9. They are furthermore the smallest, much smaller than any other recognizable type of *Iris setosa* (note fig. 1). They are short, seldom branching, with small leaves and few nodes.

This conservatism of *Iris setosa* var. *canadensis* is distinctive of most of the glacial endemics (or near endemics) of the region around the Gulf of St. Lawrence. In one of his classic contributions to the subject, Fernald ('29) has aptly characterized them as "already waning types, too old, or too conservative to spread into closely adjacent and virgin soils." In the case of *Iris setosa* var. *canadensis* the invariability cannot be a direct effect of time, for the highly variable irises of Alaska are quite as aged. It is more probably, as Professor Fernald has suggested, an innate conservatism; a conservatism founded genetically upon the fact that these irises are descendants of a small and highly selected stock. Hard times removed from the region all the luxuriant types which may once have existed there. When the ice age was over the immediate area was repeopled from the few plucky survivors. Their descendants, *Iris setosa* var. *canadensis,* bear the scars of the glacial period, so to speak, in their conservatism; an innate invariability which, on the one hand, gives them a greater uniformity, and on the other, prevents their adapting themselves readily to other environments.

In the light of its probable history, it is not surprising to find

no regional differentiation in *Iris versicolor.* If, as seems probable, it originated in interglacial times, it is a comparatively young species. It is furthermore inhabiting a region which is extremely youthful floristically, most of it not becoming available for plant occupancy until the last retreat of the Pleistocene ice. Having only recently moved into most of the territory it now occupies, *Iris versicolor* has had as yet little or no opportunity to develop geographical races within the species.

Much the same argument can be made for the northern flank of *Iris virginica* var. *Shrevei.* It is in this part of its range, thanks to irregular glacial topography, that it occurs most frequently and is therefore most easily studied. Within this area there is little or no evidence of geographical races. Were it possible to study *Iris virginica* and *Iris virginica* var. *Shrevei* in the same detailed manner on the older lands they occupy in the south, it is more than probable that considerable geographical variation would be found. There are indications of such differentiation in the few samples from these areas which are available in herbaria. A detailed statistical census would probably reveal still more.

SUMMARY

1. Most of the northern blue flags occur in more or less isolated colonies of from a few to many thousand individuals. The average frequency of such colonies per 100 square miles was found to vary from 350 in southern Michigan to 5 in Alabama and Mississippi.

2. From a statistical study of 60 colonies it is shown that there is little regional differentiation within any of the subspecies. Even within the same region, however, there are pronounced differences between the colonies.

3. The colony is an important evolutionary unit in these irises. Through its isolation each colony develops a distinctive type which is of potential phylogenetic importance.

4. It is shown that the differences between geographical varieties in these irises are of about the same order as differences between colonies. Many of the colonies carry the po-

tentialities of a variety or a subspecies, though these are seldom released by the conditions under which they exist.

5. The conservatism of *Iris setosa* var. *canadensis* is discussed in the light of its history as a glacial relict. Its comparative invariability and poor colonizing ability are probably innate as suggested by Fernald. They result genetically from the fact that this subspecies has descended from what in glacial times must have been a small population living under adverse conditions.

6. The lack of geographical differentiation within *Iris versicolor* and the northern colonies of *Iris virginica* var. *Shrevei* is correlated with their occupancy of a floristically youthful territory. *Iris virginica* var. *Shrevei* would probably reveal greater regional differences if it could be studied on floristically older lands in the south.

BIBLIOGRAPHY

Anderson, Edgar ('28). The problem of species in the northern blue flags, *Iris versicolor* L. and *Iris virginica* L. Ann. Mo. Bot. Gard. **15**: 241–332.

————, ('35). The irises of the Gaspé Peninsula. Am. Iris Soc. Bull. 59: 2–6.

Fernald, M. L. ('29). Some relationships of the floras of the northern hemisphere. Intern. Cong. Pl. Sci. Proc. **2**: 1487–1507.

Wright, S. ('31). Evolution in Mendelian populations. Genetics **16**: 97–159.

V. The Evolutionary Patterns of the Genus Iris

Students of the species problem are faced with a curious dilemma. By the nature of that problem they are forced to confine their attention to the details of a few species; yet if they do so exclusively they will be unable to interpret their results in general terms. The details of evolution vary from genus to genus and even from species to species; when one discusses the evolutionary patterns discerned by intensive work on one or two species he must attempt to determine to what extent those patterns are general characteristics of most species and to what extent they are special features of those few. Throughout the following discussion an attempt will be made to apply the information derived from these three species of *Iris* to the entire genus. It is as yet too early to consider the larger problem of speciation in the higher plants in the light of these results, except in the most general way.

In addition to the correction factor for the peculiarities of the germ-plasm one must also allow for the peculiarities of the region in which the studies were made. Speciation is a function of the region under observation. If a region is without pronounced barriers, speciation for most of the organisms in that area will be simpler than in an area with a complex system of barriers and partial barriers. It will also be affected by the age of the region. In one floristically young, geographical differentiation within species will be less intense than in regions which have been continuously available for occupancy for a long period of time. It should therefore be kept in mind during the following discussion that these studies were, for the most part, carried on in an exceedingly youthful region floristically and one in which there are no geographical barriers of any great importance.

A number of processes of evolutionary significance are taking place in these irises, all of which affect the ground-plan of the genus. Three of them, hybridization, amphidiploidy, and colonial differentiation, have produced effects which were readily perceptible by the methods used in this study. A general summary of the results is presented graphically in fig. 13.

The fundamental pattern is composed of the three species, which can be represented as great compound cables, stretched from the past into the future. For long eras these cables are practically parallel; even the detailed methods of this investigation have produced little or no evidence for the ultimate derivation of these separate cables from a common source.

Examining these cables more closely it is apparent that they are made up of smaller cords, the colonies. These cords likewise maintain their individuality for considerable time. Such a division of the species into small colonial units is probably characteristic not only of these three species but of a good part of the genus *Iris*. Certainly the other species with which I am personally acquainted in the field, *I. fulva, I. foliosa, I. prismatica, I. foetidissima, I. pseudacorus,* and *I. missouriensis,* grow in much the same sort of more or less isolated colonies.

Within this small group of irises there are three apparent cases where colonial differences have developed into geographical varieties. Very anciently the *Iris virginicae* of the Atlantic seaboard became slightly differentiated from those of the Mississippi Valley. As has been shown above, this difference is of about the same order of magnitude as that between colonies and is therefore most easily interpreted as due to some ancient geographical change which reduced one or both of these regions to one or a few colonies. By some such process also *Iris setosa* var. *interior* diverged from the *Iris setosae* of coastal Alaska and of northeastern Asia. More recently, during glacial times, *Iris setosa* var. *canadensis* was reduced to a highly inbred remnant (see pp. 495–496).

At the present time, therefore, *Iris virginica* is composed of two slightly divergent sub-cables, *Iris setosa* of three, and the youthful *Iris versicolor* is as yet but a single cable. Supposedly by the successive compounding of such divergencies, subspecific differences might be built up into differences of specific magnitude. There is little evidence in this study to contradict such a theory, but it should be pointed out that there is none to support it. In the opinion of the author the theory that geographical varieties are potential species is a debatable one.

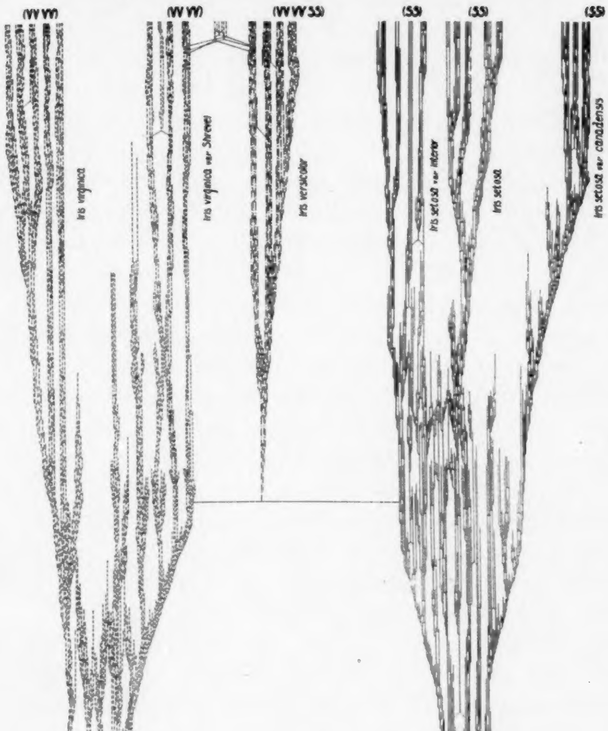


Fig. 13. Diagram showing phylogenetic relationships in the northern blue flags. Further discussion in the text.

Observation and experiment have shown (Anderson, '28) that in *Iris versicolor* and *Iris virginica* the colonies themselves are more or less divided into inbred lines, so that in these species we can speak of the colony "cords" as being made up of pure-line "threads." Since cross-pollination occurs occasionally the threads maintain their identity for only a few generations. This detail of the evolutionary pattern will vary greatly from *Iris* species to *Iris* species. There are very probably species in which inbreeding is more severe; there are certainly self-sterile species in which there is complete outcrossing. In the former the threads would be longer, in the latter there would be no recognizable threads at all within the colony cords (Anderson, loc. cit. pp. 308–310).

The great ground pattern of the cables is a simple one, with two exceptions. Very occasionally by amphidiploidy a single strand runs out from one trunk line to another and at an intermediate point a whole new cable arises. An earlier paper of this series presented detailed evidence for the amphidiploid origin of *Iris versicolor.* The secondary pairing and multiple association characteristic of the pollen mother-cells of *Iris virginica* strongly suggest that it is itself the result of an ancient amphidiploid hybridization, perhaps between a species somewhat like *Iris tripetala* and one related to *Iris hexagona.*

Such occasional interweaving of phylogenetic lines is apparently characteristic of most of the genus *Iris.* Simonet ('34) reports chromosome numbers for the section Pogoniris which suggest amphidiploidic relationships and has presented cytological proof ('35) for the occurrence of amphidiploidy in cultivated irises. As Randolph has shown (*loc. cit.*, p. 65), there is experimental evidence that in *Iris,* species with differing chromosome numbers cross more readily than in many other genera. He also presents some evidence for the functioning of unreduced gametes in *Iris.* Both of these conditions favor amphidiploidy. The presence of even occasional amphidiploidy within a genus will so complicate the phylogenetic relationships that it will be impossible to divide and subdivide it naturally into sections and subsections. We would therefore predict for the genus *Iris* that while there might be evidence of

groups of related species, it would be impossible to arrange all these groups in a clear-cut natural system. Such is actually the case. The latest monographer of the genus has the following to say about the difficulties of subdividing the section Apogon, numbering some 50–100 species and native to Europe, Asia, and North America: "It seems unfortunately impossible to select any one character or set of characters to form a guide through the maze of species. . . . The classification given below is therefore admittedly unsatisfactory partly because some of the species seem to stand by themselves and to have little or no affinity to any others" [Dykes, '13]. He then proceeds to divide the section into fifteen sub-groups. On the theory outlined above *Iris versicolor* is an amphidiploid hybrid between *Iris virginica* of his group X and *Iris setosa* of group XIV. A few relationships of this sort would produce exactly the difficulties which Dykes describes.

The other tangle in the evolutionary pattern of these irises is provided by hybridization. Though such tangles are a characteristic feature of the evolutionary pattern in the genus *Iris*, they form in this group of species a small knot of minor consequence. *Iris virginica* and *Iris setosa* are now geographically isolated, though they still in part occupy the same river system. *Iris setosa* var. *canadensis* and *Iris versicolor* grow together throughout the range of the former, but there is very great numerical isolation between them (38 vs. 108 chromosomes). Hybrids are occasionally found, but they are very rare. The only hybridization of any consequence within the group at the present time is between *Iris versicolor* and *Iris virginica*. Even in this case, there is geographical isolation between the bulk of the two species. Along the eastern seaboard, where the two species have apparently been longest in contact, they are both quite rare. It is only around the Great Lakes, where they are both exceedingly common, that hybridization is at all common. Even here there is partial isolation for the blooming periods of the two species barely overlap. At the northern end of the southern peninsula of Michigan, the two species have evidently been closely associated throughout much of post-glacial time (Anderson '33) and their areas of contact, due to the

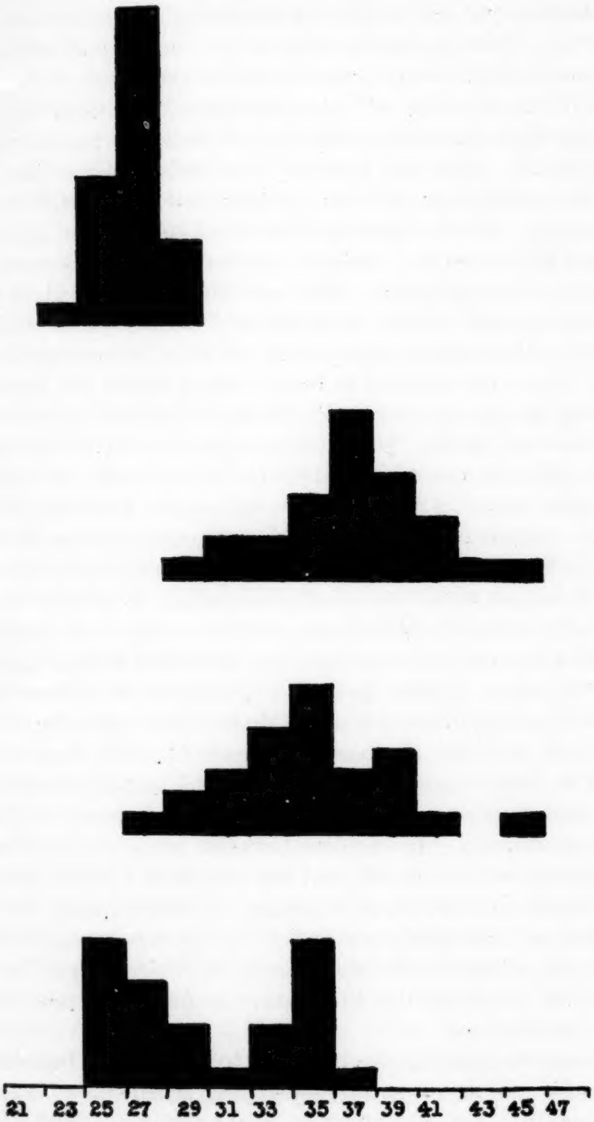


Fig. 14. Frequency distribution for the index, sepal length/petal length + sepal width/petal width, for 27 plants each from the following colonies: Pardeeville, Wisconsin *(Iris virginica* var. *Shrevei)*; Billings Bridge, Ottawa, Canada *(I. versicolor)*; Engadine, Michigan (hybrids); St. Ignace, Michigan (hybrids).

peculiarities of the various post-glacial lakes, are extremely involved. Even in this area the great majority of colonies are composed exclusively of one species or the other.

On the north shore of Lake Michigan, in an area with a similar post-glacial history, two hybrid colonies were studied in some detail. One was located three miles west of St. Ignace and has since been partially obliterated by relocation of the state road. At this location there were to be found apparently normal *Iris versicolor* and *Iris virginica* and a large number of peculiar intermediates. Few of these resembled the first-generation and second-generation hybrids which had been raised in the experimental plots. Most of them, on the other hand, were very similar to back crosses which had been made between the first-generation hybrids and the two species. This is borne out by fig. 14 where representative colonies of each species are contrasted with these two hybrid colonies, using the following index as a basis for comparison: sepal length/petal length + sepal width/petal width. Figure 14 also shows the very different condition which was encountered at the other hybrid colony which was studied in detail. It was located just west of Engadine, Michigan, and was composed entirely of plants which closely resembled the artificial F_1 hybrids of the breeding plot. Since they also presented the characteristic vigor of such hybrids it is probable that they were for the most part such hybrids, the parental species having been exterminated by their vigorous offspring. It is not impossible, however, that they may represent some new balanced combination of chromosomes. In crosses between such complex amphidiploids as *Iris versicolor* and *Iris virginica* various new polyploid types are not at all unlikely. Unfortunately, the large numbers of chromosomes and the very short period during which the reduction division can be studied (only a few days out of the year) render this rather unprofitable material for such examination.

One can summarize the effect of hybridization between *Iris versicolor* and *Iris virginica* by saying that it does occur very occasionally. Its only effect so far has been a slight blurring of the two species along the zone of contact. It does, however,

provide a means by which new polyploid hybrid species might eventually arise.

Were there fewer technical difficulties involved a detailed analysis of hybridization in these irises would be well worth while, since hybridization is a characteristic part of the phylogenetic pattern throughout the genus. The remarkable phylogenetic tangle of species and hybrids discovered in the Mississippi delta by Dr. J. K. Small is by no means exceptional. Much the same situation exists among the Pogoniris species around the Mediterranean; the irises of the Spuria group apparently behave in the same way in western Asia; it was perhaps from some such complex that the Japanese irises had their beginnings.

Because hybridization is apparently such an important phylogenetic factor in the genus *Iris*, the hybrids of the Mississippi delta deserve careful analytical study, genetically, taxonomically, and cytologically. It is not enough to prove that hybridization is taking place. Much more important is the determination of its exact role among the Louisiana irises.

The effects of hybridization are various according to the peculiarities of the germ-plasm upon which it is operating and the external conditions under which it takes place. It may result in new amphidiploid species such as *Iris versicolor*. It may produce intermediate swarms which obliterate previous specific boundaries. It may increase the variability of one of the parental species by introducing a small proportion of germplasm from the other (Anderson & Woodson, '35, p. 37).

Possibly all of these processes are taking place among the Louisiana irises. It should not be difficult to determine their relative importance and ultimate phylogenetic effects. These irises possess a number of technical advantages for such a study. They have comparatively low chromosome numbers; they are easy to cultivate in experimental gardens; they possess conspicuous specific differences. They are, as Viosca has said ('35), "uniquely adapted for the study of experimental evolution" and one may join with him in predicting a "bright future for them in the study of biology."

To summarize: the evolutionary patterns of the blue flags are fairly typical of the genus as a whole. Seen in a greatly foreshortened view they can be represented graphically as in fig. 13. They form a somewhat tree-like system of cables, the ground pattern occasionally made more complex by amphidiploid cross-connections. The pattern is complicated at one point by inter-specific hybridization. The cables themselves are divided into distinctive cords, the colonies.

Much the same set of patterns would characterize the entire genus *Iris*. The complex knots due to interspecific hybridization would be larger and more significant in certain other portions of the genus; in certain sections the cross-connections of amphidiploidy would be lacking altogether; in a few sections they might be somewhat commoner. All in all, however, fig. 13 may be taken as a fairly accurate representation of phylogenetic relationships for the whole genus. This general similarity of evolutionary patterns within the genus rests upon the fact that the germ-plasm of any species of the genus *Iris* is not a vague generalized germ-plasm. It is **Iris** germ-plasm. It has a number of inherent characteristics which affect speciation and which cause the details of speciation, to be similar throughout (Anderson, '31). It is a genus in which amphidiploidy occasionally occurs, in which every species has a strong development of vegetative propagation, in which interspecific fertility is the rule. It is, on the other hand, a genus which is ecologically conservative.

Species after species exhibits rather precise demands as to habitat and seems unable to produce variants adapted to more or less moisture, more or less shade, more or less acidity. In the genus *Aquilegia* every species which I have studied extensively is richly provided with ecotypes; sun-forms, shade-forms, types inherently adapted to sour, wet swamps, to sunny, limestone cliffs, to sand dunes, and to woodlands. In *Iris versicolor* and *Iris virginica,* in spite of intensive search, I have been unable to recognize a single ecological variant. Like many genera of the Liliiflorae, the order to which they belong, they are curiously unamenable to ecological differentiation. This conservatism, since it characterizes the whole genus, must rest

upon some inherent property of *Iris* germ-plasm. What that property may be we cannot, as yet, even hazard a guess. It may be that the germ-plasm of *Aquilegia* varies in a way that is unknown or uncommon to the germ-plasm of *Iris*. It may be that due to its ontogenetical organization the genus *Iris*, though possessing the same basic kinds of germinal variation as the genus *Aquilegia*, will nevertheless not respond with variants equipped for other habitats.

BIBLIOGRAPHY

Anderson, Edgar ('28). The problem of species in the northern blue flags, *Iris versicolor* L. and *Iris virginica* L. Ann. Mo. Bot. Gard. **15**: 241–332.

————, ('31). Internal factors affecting discontinuity between species. Am. Nat. **65**: 144–148.

————, ('33). The distribution of *Iris versicolor* in relation to the post-glacial Great Lakes. Rhodora **35**: 154–160.

————, and Robert E. Woodson ('35). The species of Tradescantia indigenous to the United States. Arn. Arb. Harv. Univ. Contr. 9: 132 pp.

Dykes, W. R. ('13). The genus Iris.

Randolph, L. F. ('34). Chromosome numbers in native American and introduced species and cultivated varieties of Iris. Am. Iris Soc. Bull. 52: 61–66.

Simonet, Marc ('34). Nouvelles recherches cytologiques et génétiques chez les Iris. Theses Fac. Sci. Paris, No. 15: 229–383.

————, ('35). Conjugaison autosyndétique des chromosomes. Bull. Biol. France et Belg. **69**: 178–212.

Viosca, Percy Jr. ('35). The irises of southeastern Louisiana. Am. Iris Soc. Bull. 57: 3–57.

HYBRIDIZATION IN AMERICAN TRADESCANTIAS

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FOREWORD

Widely different opinions are held by present-day biologists as to the evolutionary importance of hybridization between species. One of the main reasons for the disagreement seems to be the lack of summarized and codified data bearing upon the problem. This series of papers is not an attempt either to prove or disprove the *importance* of hybridization. It is rather an attempt to gather pertinent data from which to analyze the *effects* of hybridization.

The genus *Tradescantia* has been chosen for two main reasons: (1) Previous taxonomic, cytological, and genetical studies (Anderson and Woodson, '35; Anderson and Sax, '36; Anderson, '36) have indicated the main outlines of the situation in this genus; (2) *Tradescantia* for purely technical reasons is a better object for such investigations than are many other genera of the higher plants, chief among its assets being the facility with which it can be studied cytologically and the ease with which most of the species can be brought into cultivation.

The main object of the investigation, as stated above, has been to procure data from which the importance and the evolutionary rôle of hybridization could be estimated and demonstrated. It had previously been experimentally determined that most of the species allied to *T. virginiana* could be hybridized and that their hybrid progeny were semi-fertile. Similar hybrids had been found in the field and had been subjected to detailed morphological and cytological analysis, but such work was purely preliminary. It merely demonstrated the occurrence of hybridization. What was needed was a method which would determine the dynamics of hybridization in natural populations. In mathematical terms it was necessary to ascertain the frequencies as well as the range of variation (Anderson

and Turrill, '35). That is to say, that we needed to measure and record the effect of hybridization upon the entire population in which it was occurring. Such a method has been evolved and is outlined in section I, while its application to a particular case is demonstrated in section II.

I. A Method for Measuring Species Hybrids

Biology employs two methods of measurement, the quantitative and the qualitative. Each has its advantages and disadvantages. Two of the main objections to purely quantitative methods are: (1) quantitative scales are arbitrary and may not bear a direct relation to the phenomenon under investigation, (2) the observational basis of purely quantitative methods is too narrow for many biological problems. It may be well to amplify these *dicta*.

(1) The chief purposes of the quantitative method are to record the variation of certain phenomena and from this record to analyze the forces producing the variation. If a scale has been chosen which is an accurate reflection of the main underlying factors, then the analysis will be a comparatively simple matter. But if the scale used is not in harmony with these underlying causes then it may be difficult, or impossible, to analyze the data. In other words, the data are then no more than a record; a qualitative measure, if objectively defined, would have been quite as efficient. In a paper of fundamental biological significance Wright has demonstrated ('26) how even as simple a transformation as a percentage scale can obscure the interpretation of quantitative data. In many biological problems the customary quantitative scales in which the original observations are recorded are even more inefficient and misleading. The fact that centimeters are equally spaced on the ruler does not mean that variations of a centimeter are always of equal biological magnitude when we use that ruler to measure plants and animals. Purely quantitative measures, lengths, areas, weights, etc., are superior to qualitative units only when they reflect more or less directly the changes in the underlying factors.

(2) As has been pointed out by Minot ('11), the observa-

tional basis of purely quantitative methods is often too narrow for studying biological phenomena. A set of weights, or lengths, is too insignificant an observation to yield sufficient data for exploring a problem. Biology has advanced most rapidly when appropriate qualitative measures have been developed and used with precision. In Genetics, for example, the fundamental data are qualitative. Once obtained they are treated with such precision that most geneticists probably think of their work as purely quantitative. But the fundamental categories, "vestigial" vs. "non-vestigial," "scute" vs. "non-scute," "forked" vs. "non-forked," etc., are quite as qualitative as the fundamental categories of taxonomy. It is because of this fact that they are a broad enough tool to yield useful information about such a complex phenomenon as heredity. If the methods of Drosophila genetics were purely quantitative the flies would not be classified in qualitative categories, but their wing lengths, eye diameters, etc., would be laboriously measured. Imagine the difficulties of conducting a Drosophila experiment involving two or three wing mutants in which the only available data were the lengths and breadths of the wings! Genetics has been able to advance because it was willing to take the Mendelian recessive (a qualitative unit about whose ultimate significance relatively little was known) and to use that unknown but recognizable entity as a basic unit.

For the study of the species problem a similar combination of qualitative and quantitative methods seems desirable. Few of the differences between species are of the simple sort which are readily amenable to quantitative treatment (Anderson and Whitaker, '34). This is not to say that species do not differ quantitatively. They do, just as do the wing mutants of Drosophila, but in both cases it is more efficient to use qualitative categories.

Purely qualitative methods, however, have their own disadvantages. They are often said to be more subjective, but this point is open to argument. Certainly the gene differences by which Drosophilae are scored are quite as objective as quantitative measurements. A very real disadvantage in purely qualitative work is that it is not commensurate. One cannot with purely qualitative methods make an accurate com-

parison of the *Iris* plants of one meadow with those of another. What we need for the species problem is a method whose fundamental observations are based upon the qualitative categories of taxonomy but which treats these categories in such a way that they can be used for comparison and analysis. This has been done below in a fairly simple fashion by constructing an index which is the resultant of all the qualitative characters which are readily available.

In the simplest possible case the method operates as follows: Given two species, A and B, the hybridization between which is the object of investigation. Given n readily ascertainable differences between A and B (as, for instance, position of inflorescence, nature and distribution of pubescence, number of nodes to the stem, distribution of stomata, etc.). For each of these characters an individual plant can be scored as 'a' (like species A); as 'b' (like species B), or as 'i' (intermediate, preferably the actual F_1 if that has been obtained). In particular cases it will be possible to define two or more intermediate grades for the character in question. A hybrid population will be scored somewhat as follows in a case where six distinguishing characters were available:

plant no. 1: a-a-a-i-a-a
plant no. 2: a-a-i-i-b-i
plant no. 3: i-i-i-i-i-i
plant no. 4: b-i-i-i-b-a

and so on for all the plants which are scored. To summarize the population as a whole, all that is necessary is to turn this qualitative scoring into a quantitative index. An index running from complete "A-ness" to complete "B-ness" can be made by arbitrarily giving every 'a' the value of 0, every 'b' the value of 2, and every 'i' the value of 1. This will produce a scale with $2n + 1$ divisions (in this case 13, i. e., 0 to 12 inclusive. An individual of species 'A' would have an index value of 0 $(0 + 0 + 0 + 0 + 0 + 0)$, while an individual of species 'B' would have a value of 12. Plant no. 1 in the above example will have an index value of 1; plant no. 2 a value of 5; plant no. 3 a value of 6; plant no. 4 a value of 7. When the values of each plant

have been computed they can be summarized as a frequency distribution. The frequency distribution constitutes a record of the whole population, in so far as these two species and mixtures between them are concerned. It can be used for the comparison of different hybrid populations and to discover and analyze the forces which are at work in such populations. The index can be varied to fit the available data in various ways. When, for instance, certain of the categories are thought to be more or less reliable than the others they can be appropriately weighted in combining the index. The method seems capable of producing useful and unique data in regard to the variation within and between species. I have used it extensively in the genus *Tradescantia,* one case being published in the second part of this paper. I have also applied it successfully to the analysis of hybridization in *Amelanchier* and *Baptisia* (unpublished). Dr. H. P. Riley has applied it to the hybrid *Iris* populations of the Mississippi delta with interesting results (Riley, in press).

After I had originated the method Dr. Jens Clausen very kindly called my attention to a paper by Raunkiaer ('25) in which an almost identical method of recording the qualitative categories had been applied to a case of hybridization in *Crataegus.* He had not, however, performed the further step of turning the qualitative record into an index, thus making it possible to summarize the population. When this is done the case proves to be a particularly interesting one with certain unique features.

SUMMARY

The advantages and disadvantages of quantitative and qualitative methods in biology are discussed. A method of summarizing hybrid populations is developed which utilizes qualitative categories for its initial observations and from these computes a quantitative index value.

II. Hybridization between T. virginiana and T. canaliculata

The method developed in Section I has already been applied to numerous cases of hybridization in *Tradescantia.* The fol-

lowing one has been selected for preliminary demonstration because it has been analyzed in greater detail and because it is a relatively simple case with no such complicating factors as differences in chromosome number.

Tradescantia virginiana L. and *T. canaliculata* Raf. (*T. reflexa* Raf.) are the two commonest Tradescantias of eastern North America. Although each can be cultivated under a variety of conditions they are usually found growing naturally in quite different situations; *T. canaliculata* in the sun, often upon or near rocks or in dry sands; *T. virginiana* in shade or semi-shade. Until white civilization disturbed their natural relationships they seldom or never occupied the same habitat. Even at the present time active hybridization is confined to a very small proportion of either species. The outstanding morphological differences between the two species are as follows (those characters marked with an asterisk * require the use of a good hand-lens):

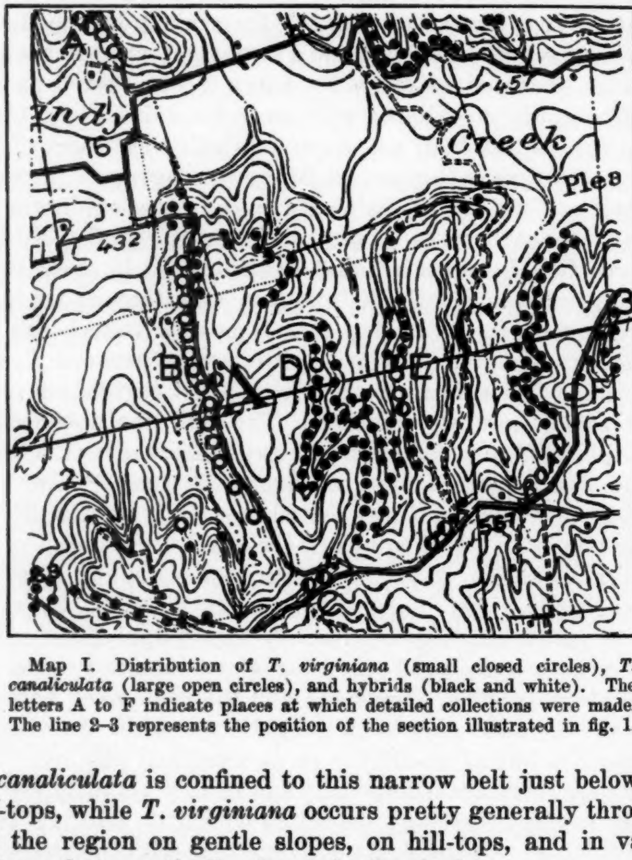
	T. virginiana	Index value	*T. canaliculata*	Index value
(1)	2–3 nodes	2	6–8 nodes	0
(2)	Sepals broadly ovate, apex broadly acute; calyx inflated after anthesis	2	Sepals elliptic, apex narrowly acute; calyx not inflated after anthesis	0
(3)	Sepals and pedicels pubescent throughout	3	Pedicels glabrous; sepals glabrous or barbate	0
(4)	* Stomata no more conspicuous than the cells of the upper epidermis	1	* Stomata (and subsidiary cells) much more conspicuous than the cells of the upper epidermis	0
(5)	* Stomatal areas of the upper epidermis narrower than the areas without stomata	1	* Stomatal areas much broader than the areas without stomata	0
(6)	* Longitudinal distance between stomata longer (often several times as long) than the diameter of a stoma	1	* Longitudinal distance shorter than the diameter of a stoma	0
	Total index value	10		0

It was a relatively simple matter to turn these characters into an index, according to the method developed in section I. The figures to the right show in each case the index value assigned to that character. In the case of (3) it was possible to recognize two intermediate grades. If the pedicel was weakly pubescent and the calyx showed the beginnings of a barbate tuft at the apex it was scored as 'vi' (virginiana-intermediate) with an index value of 2; if it had a strongly developed barbate tuft with scattered hairs on the calyx it was scored as 'ci' (canaliculata-intermediate) with an index value of 1. Categories (4), (5), and (6) are given only half the weight of the previous three since they are all different measures of the same quality, the distribution of stomata on the upper epidermis.

It is certainly true of *Tradescantia,* as Wiegand ('35) has observed for *Amelanchier,* that hybridization is much more frequent in areas greatly disturbed by man than under more natural conditions. For that reason an area was chosen for detailed examination in which hybridization between *T. virginiana* and *T. canaliculata* was for the most part taking place under nearly natural conditions. The spot finally chosen is illustrated in Map 1. It is an area two miles square in the township of Joachim, in Jefferson County, Missouri. After the area had been selected it was visited repeatedly by foot and by automobile in an effort to record the exact distribution of all the Tradescantias within the four square miles selected. The region is a low plateau, very much dissected by small streams which flow into the near-by Mississippi River. The land has been under cultivation for over a hundred years, the flat hill-tops (plateau remnants) and the rich valley bottoms being for the most part in cultivated crops while the steeper hillsides are left as woodlands or as woodland pasture. The underlying rocks are sedimentary and lie in practically the positions in which they were deposited with little faulting, folding, or tilting. All the strata are limestone with the exception of the St. Peter's Sandstone, here a soft gray-white stone usually exposed as a more or less perpendicular cliff capped with resistant limestone.

The stratigraphy is of considerable importance to the prob-

lem in hand, for it is these steep limestone and sandstone cliffs which constitute the natural habitat for *T. canaliculata.* They are so rocky and dry that not even in the original forest were they fully covered with trees, particularly on southern and western slopes. It will be seen on the map and in fig. 1 that



Map I. Distribution of *T. virginiana* (small closed circles), *T. canaliculata* (large open circles), and hybrids (black and white). The letters A to F indicate places at which detailed collections were made. The line 2–3 represents the position of the section illustrated in fig. 1.

T. canaliculata is confined to this narrow belt just below the hill-tops, while *T. virginiana* occurs pretty generally throughout the region on gentle slopes, on hill-tops, and in valley bottoms, but practically always in the shade.

In this particular area *T. virginiana* was much more common than *T. canaliculata.* An effort was made to estimate relative frequencies by computing from the map the areas occupied by

T. virginiana, T. canaliculata, and the hybrids. These were found to be 16 : 1 : 0.5 respectively.

Thirty plants each of *T. virginiana* and *T. canaliculata* were scored at the localities marked as 'F' and 'B' on the map. The pure species, as can be seen from table I and fig. 2, were relatively invariable and agreed with scorings made at other points in their range. A few hybrid plants were found along the zone of contact between the two species and large hybrid colonies, consisting of fifty or more individuals, occurred at four places, labeled A, C, D, and E on the map. Detailed studies were made at the first two localities.

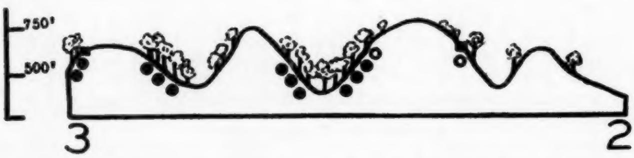


Fig. 1. Diagrammatic section (to scale) along line 2–3 in Map I. Figures to the left show feet above sea-level; closed circles represent *T. virginiana* and open circles *T. canaliculata.* The line is slightly over 2 miles long.

Locality A. At this point the public road starts up onto Sandy Ridge along the hard limestone which caps the St. Peter's Sandstone. The latter forms a series of much-weathered cliffs slightly to the south of the road and while the area is pastured, it has not been greatly disturbed of late years. At various points along the cliff a few plants of *T. canaliculata* are growing, and as the road swings to the right the cliffs and the ledge become somewhat shadier by reason of the narrow gorge cut back into the hill by an intermittent stream. At the head of the gorge there is an interesting area of a few hundred square feet in which many kinds of habitats and hence many kinds of plants are brought into close juxtaposition. Rock-plants, prairie grasses, woodland and even desert species are found within a few feet of each other. It is, in other words, exactly the situation in which one might logically expect to find hybridization between ecologically isolated species. Trades-

TABLE I

SCORING OF INDIVIDUAL PLANTS AT THREE LOCALITIES IN JEFFERSON COUNTY, MISSOURI. FURTHER EXPLANATION IN TEXT.

Plant no.	Categories						Total	Plant no.	Categories						Total
	(1)	(2)	(3)	(4)	(5)	(6)			(1)	(2)	(3)	(4)	(5)	(6)	
Locality B—*T. virginiana*															
1	v	v	v	v	v	v	11	16	v	v	v	v	v	i	10½
2	v	v	v	i	v	v	10	17	v	v	v	v	v	v	11
3	v	v	v	v	v	v	11	18	v	v	v	v	v	v	11
4	v	v	v	i	i	v	9½	19	v	v	v	v	v	v	11
5	v	i	v	v	v	v	10	20	v	v	v	v	v	v	11
6	v	v	v	v	v	v	11	21	v	v	v	v	v	i	10½
7	v	v	v	v	v	v	11	22	v	v	v	v	v	v	11
8	v	v	v	i	v	v	10	23	v	v	v	v	v	v	11
9	v	v	vi	i	v	v	9	24	v	v	v	v	v	v	11
10	v	i	v	v	v	v	10	25	v	v	v	v	i	v	10½
11	v	v	v	v	v	v	11	26	v	v	v	v	v	i	10½
12	v	i	v	v	v	i	9½	27	v	v	v	v	i	v	10½
13	v	v	v	v	i	v	10½	28	v	v	v	i	v	i	9½
14	v	v	v	v	i	v	10½	29	v	v	v	v	v	v	11
15	v	v	v	v	v	v	11	30	v	v	v	v	v	v	11
Locality F—*T. canaliculata*															
1	c	c	c	c	c	c	0	16	c	c	c	i	i	c	1½
2	c	c	c	c	i	c	½	17	i	c	c	c	c	c	1
3	c	c	c	c	c	c	0	18	c	c	c	i	c	c	1
4	c	c	c	c	i	c	½	19	c	c	c	i	i	c	1½
5	c	c	c	c	c	c	0	20	i	c	c	c	c	c	1
6	i	c	c	i	c	c	1½	21	c	c	c	c	i	c	½
7	c	c	c	i	c	c	1	22	c	c	c	c	c	c	0
8	c	c	c	i	i	c	1½	23	c	c	c	c	c	c	0
9	i	c	c	c	c	c	1	24	i	c	c	c	c	c	1
10	i	c	c	c	c	c	1	25	i	c	c	c	i	c	1½
11	c	c	c	c	c	c	0	26	c	c	c	c	c	c	0
12	c	c	c	c	i	c	½	27	c	v	c	c	c	c	0
13	c	c	c	c	c	c	0	28	c	c	c	i	c	c	1
14	c	c	c	i	c	c	1	29	i	c	c	c	c	c	1
15	c	c	c	i	c	c	1	30	c	c	c	c	i	c	½
Locality A—*T. virginiana* x *T. canaliculata*															
1	v	c	ci	c	i	v	3½	16	i	i	vi	i	i	i	6
2	i	c	ci	c	i	c	2½	17	c	c	ci	v	i	i	4
3	i	c	vi	c	i	c	3½	18	i	c	ci	c	i	i	3
4	i	c	ci	c	c	c	2	19	i	i	vi	c	i	i	5
5	i	c	ci	i	i	i	5	20	i	c	ci	i	i	c	3½
6	i	i	vi	c	i	i	5	21	i	i	ci	v	v	c	6
7	i	i	c	c	c	i	2½	22	i	i	vi	v	v	i	9½
8	i	i	ci	v	c	v	6	23	i	c	vi	i	i	c	4½
9	i	c	ci	c	c	i	2½	24	i	i	vi	v	v	i	7½
10	i	c	c	i	i	c	2½	25	i	c	v	i	i	c	5½
11	i	v	ci	c	i	i	5	26	c	c	vi	v	c	i	4½
12	i	v	vi	c	i	i	5	27	i	v	vi	v	v	i	8½
13	i	c	ci	i	i	c	3½	28	i	i	v	c	i	v	6½
14	i	i	c	c	i	i	3	29	i	i	v	v	v	i	7½
15	c	i	c	c	i	c	1½	30	i	c	c	v	c	c	3

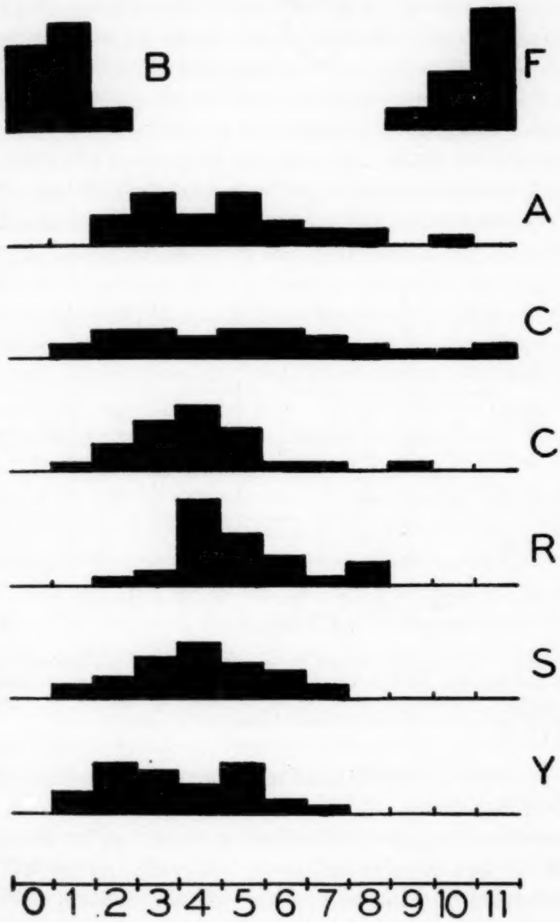


Fig. 2. Frequency distributions for the *virginiana-canaliculata* index. Thirty plants each collected at localities A, B, C (two terraces), and F illustrated in Map I; R and S at Algonquin Station, Y at Maplewood, Missouri. Index values shown on the scale at the base of the diagram. B represents a population of pure *T. canaliculata*, F a population of pure *T. virginiana;* the remainder hybrid populations. Further explanation in the text.

cantias occur rather generally over the whole area; a few plants of apparently straight *T. virginiana* are growing in the shade of the red cedars and a mongrel population of *T. virginiana* × *T. canaliculata* grows in the sunny and semi-shady situations. The cliff at this point is so steep that it was impracticable to collect plants in quantity from the cliff-sides but all of those growing on the ledge were scored in detail. The results are presented in table I and fig. 2, A. (In presenting the frequency distributions only the first thirty plants have been

SCALE VALUE \ LIGHT INTENSITY	1-2	3-4	5-6	7-8	9-10	
0-1			1			
2-3	2	1	2	4	4	
4-5	2	5	2	4	3	
6-7	5	4		2	2	
8-9				2		

Fig. 3. Correlation between scale value and the light intensity of the habitat for 46 hybrid plants at locality A. Light intensity in parts of a second required for an equivalent exposure (i. e., scale runs from very shady at left to full sun at the right).

utilized in order to facilitate frequency comparisons with the other distributions.)

The peculiar frequency distribution exhibited by the hybrids at locality A has been found to be generally characteristic of hybrid colonies of *T. canaliculata* × *T. virginiana*. It can be conveniently, if somewhat loosely, described by saying that in such populations the hybrids "absorb" the *T. canaliculata* completely but that *T. virginiana* tends to persist in a more or less pure state. It will be seen from fig. 2 that there are no absolutely pure *T. canaliculatae* in spite of the fact that the bulk of the population is much closer to that species than to *T. virginiana*. These must largely be plants which are ¾ or

$\frac{7}{8}$ or $\frac{15}{16}$ *T. canaliculata.* At the other end of the scale there is a small proportion of *T. virginiana* but very few or none of the $\frac{3}{4}$, $\frac{7}{8}$, and $\frac{15}{16}$ *T. virginiana.* As to why the two species should react in this matter one cannot as yet even hazard a guess. Since most of the hybrid populations made up of these two species react in about the same fashion, the reason is probably internal. There seems to be some force or forces which inhibits free recombination between the hybrids and *T. virginiana* and encourages such recombination between the hybrids and *T. canaliculata.* It might possibly be differential pollen-tube growth; it might be a markedly different span of life (both species are perennial); it might be a result of the differences in blooming season (i. e. *T. virginiana* blossoms early and *T. canaliculata* blossoms late. If the hybrids very largely bloomed within the flowering period of the latter species it might produce the observed result).

Among the hybrids those morphologically most like *T. canaliculata* seemed to be growing in the sunniest locations and those most like *T. virginiana* in the shadiest. An attempt was made to measure this objectively and the results are presented in fig. 3 in the form of a correlation table between light intensity and index value. The former was measured with a light meter on a day of uniform cloudiness. The meter was held a foot above the inflorescence and gave readings in fractions of a second required for equivalent exposures. As will be seen from fig. 3, the results indicate that among the hybrids (the pure *T. virginiana* having been excluded) the deeper the shade the greater is the tendency to resemble *T. virginiana.*

At *Locality C* hybridization has produced very similar results. It is a less desirable spot for detailed study since it is adjacent to a state road whose position has been repeatedly shifted and the immediate environment in which the hybrids are found has been subject to violent alterations during the last half century. The cliffs at this point form a series of narrow terraces ten to twenty feet wide and several hundred yards in length. Where the hybrids occur each terrace has evolved a more or less characteristic type. Two collections made on the upper terrace at intervals of fifty feet gave nearly identical

frequency distributions, while nearly adjacent collections from successive terraces showed different distributions. Natural selection is apparently working upon the hybrid population to produce these very local differences. Were this locality less subject to frequent and profound disturbances it would merit a much more detailed analysis.

Localities D and E were discovered too late in the flowering season to receive more than a preliminary survey. They apparently present the same general picture as did A and C.

Tradescantia virginiana and *T. canaliculata* also hybridize when growing as weeds along railroad rights-of-way, on vacant lots in the city, etc. Several such populations were examined in and near the city of St. Louis in the spring of 1936. Throughout this area *T. canaliculata* is the common weed *Tradescantia*, sometimes occurring along railroad embankments as the predominant plant of early summer for distances of several miles. Occasionally, however, in the immediate neighborhood of open oak woods, *T. virginiana* also contributes to the weed population. Two such hybrid colonies were investigated. Near the Algonquin Station of the Missouri Pacific Railroad two samples (R and S, fig. 2) of thirty plants each were collected between the railroad track and the highway. In Maplewood a sample of thirty (Y, fig. 2) was collected from a vacant lot adjacent to the electric railway. It will be seen that, as in the case of the collections made in Jefferson County, the bulk of the population is composed of individuals which score from 3 to 5 on the scale, individuals in other words which must be about ¾ to ⅞ *T. canaliculata*. Hybridization between *T. virginiana* and *T. canaliculata* both along the cliffs and the railroad tracks tends to produce a somewhat variable "*sub-canaliculata.*"

SUMMARY

Hybridization between *T. canaliculata* and *T. virginiana* was studied at seven localities in Missouri. At these localities there seemed to be a general tendency for the hybrids to "absorb" *T. canaliculata* though *T. virginiana* may persist in a pure state as a small percentage of the population. This is

interpreted as the result of a force or forces, as yet undetermined, which inhibit free recombination between the hybrids and *T. virginiana* and encourage such recombination with *T. canaliculata.*

A general discussion of hybridization is deferred until further cases have been investigated. From data already at hand it is apparent that hybridization, as previously suspected, is very widespread in the genus *Tradescantia.* The details differ somewhat with the conditions of the environment and very greatly according to the species taking part. In certain cases, at least, the resultant variability is so widespread throughout the species, that it must constitute the chief raw material for natural selection. As such it deserves exhaustive observation and critical analysis.

BIBLIOGRAPHY

Anderson, Edgar ('36). A morphological comparison of triploid and tetraploid interspecific hybrids in Tradescantia. Genetics **21**: 61–65.

————————, and Karl Sax ('36). A cytological monograph of the American species of Tradescantia. Bot. Gaz. **97**: 433–476.

————————, and W. B. Turrill ('35). Biometrical studies on herbarium material. Nature **136**: 986.

————————, and T. W. Whitaker ('34). Speciation in Uvularia. Arn. Arb. Jour. **15**: 28–42.

————————, and R. E. Woodson ('35). The species of Tradescantia indigenous to the United States. Arn. Arb. Contr. **9**: 1–132.

Minot, C. S. ('11). The method of science. Science **33**: 119–131.

Raunkiaer, C. ('25). Ermitageslettens Tjørne. Isoreagentstudier I. Kgl. Danske Videnskab. Selskab. Biol. Meddel. **5**: 1–76.

Wiegand, K. M. ('35). A taxonomist's experience with hybrids in the wild. Science **81**: 161–166.

Wright, Sewall ('26). A frequency curve adapted to variation in percentage occurrence. Jour. Am. Statistical Assn. **1926**: 162–178.